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BY
WILLIAM ARTHUR SLEDGE
University of Leeds

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THE DRYOPTEROID FERNS OF CEYLON

By W. A. SLEDGE

THE Dryopteroid ferns are here understood as comprising the subfamily Dryopteridoideae of Holttum's family Dennstaedtiaceae. This corresponds with Pichi-Sermolli's Aspidiaceae excluding those genera treated as Dennstaedtiaceae subfamily Tectarioideae by Holttum. Four genera and twenty species are represented in Ceylon. The distinguishing characters of the Dryopteroid ferns and their relationships have been discussed by Holttum in *Journ. Linn. Soc.*, Bot. 53 : 123–158 (1947) and in *Biol. Rev.* 24 : 267–296 (1949).

Typical examples of *Dryopteris, Polystichum* and *Arachniodes* are readily distinguishable but these genera are not always clearly separable since each includes species which display characters normally associated with the others. Their delimitation and circumscription is the most troublesome taxonomic problem in this group of ferns. Nor can cytology be referred to as a court of appeal in borderline cases since all three genera have the same basic chromosome number. Apart from the monotypic genus *Diacalpe* (here combined with *Peranema*), all were included under *Lastrea* and *Polystichum* in Beddome's *Handbook to the Ferns of British India, Ceylon and the Malay Peninsula* (1883). The most recent discussions bearing on the taxonomy of this group are those of Morton (in *Amer. Fern Journ.* 50 : 145–149 (1960)) and Tindale (in *Contr. N.S.W. natn. Herb.* 3 : 89–90 (1961) ; *op. cit., Flora Series* 208–211 : 55–58 (1961)).

I have not attempted in this account to add to these discussions ; to do so would require a wider knowledge of the genera than I possess. Generic descriptions are given only in generalized terms since the more detailed the descriptions the more open they become to exceptions and hence the more necessary it becomes to qualify many of the characters enumerated. My concern is to give a revised account of the group at the specific level, for as with Ceylon ferns in general very little critical attention has been paid to them for close on a century. Where generic transferences have been made the reasons for doing so are fully discussed under the species concerned.

My grateful thanks are due to the Directors and Curators of the following institutions for access to or for the loan of specimens in their charge.

B	Botanisches Museum, Berlin-Dahlem
BM	British Museum (Natural History)
CGE	Botany School, University of Cambridge
E	Royal Botanic Gardens, Edinburgh
GL	Department of Botany, University of Glasgow
K	Royal Botanic Gardens, Kew
L	Rijksherbarium, Leiden
PDA	Department of Agriculture, Peradeniya
US	United States National Museum, Smithsonian Institution, Washington DC
W	Naturhistorisches Museum, Vienna

1. *PERANEMA* D. Don

PERANEMA D. Don, Prodr. Fl. Nepal. : 12 (1825).—Nayar & Kaur in Bull. natn. bot. Gdns Lucknow 81 : 5 (1963).

Rhizome erect, scaly, fronds fascicled ; lamina broad at the base, 3–4 pinnate, axes clothed with a mixture of scales and jointed hairs, veins free ; sori medial on the acroscopic veinlets, globose, pedicellate or sessile ; receptacle hemispherical ; indusium inferior, globose, enclosing the sorus and rupturing from above.

1. ***Peranema aspidioides*** (Blume) Mett., Fil. Lechl. 2 : 33 (1859).

Diacalpe aspidioides Blume, Enum. Pl. Jav. : 241 (1828).—Bedd., Handb. Ferns Brit. Ind. : 18, fig. 7 (1883).

Rhizome erect, fronds tufted, 50–100 cm in length. Stipes about equalling the lamina, scaly, especially about the base, the scales lanceolate or linear, attenuate, entire, dark brown ; upper part of stipe and rhachis rough, scaly about the axils of the pinnae, elsewhere the axes clothed mainly with jointed hairs. Lamina mostly tripinnate, quadripinnate below, ovate or triangular-ovate in outline, gradually narrowed upwards, dark coloured, texture herbaceous ; pinnae shortly stalked, patent or ascending, the lowermost largest, up to 20 cm long, opposite or subopposite and basiscopically enlarged, the rest becoming alternate upwards ; pinnules oblong, pinnate or bipinnate below with the segments cuneate based and toothed above, upper surface with scattered slender hair-like scales, lower surface with small clavate, red glands on the veins. Sori globose, sessile, mostly one to each segment, medial on the acroscopic vein, indusium firm, membranaceous, bursting irregularly from the top. Spores monolete, plano-convex with a perispore forming an undulate wing and irregular surface folds or ridges.

CEYLON : *Thwaites C.P. 3282* (BM ; K ; PDA, 2100 m, Nuwara Eliya, April 1856, *Bradford*). Nuwara Eliya, 1950 m, 11 March 1954, *Schmid 1499* (BM). Horton Plains towards Bogawantalawa, Sept. 1890, no collector's name (PDA). Horton Plains, in shady gully in forest, 2100 m, 20 Dec. 1950, *Sledge 676* (BM ; K). Same locality, 30 Dec. 1950, *Holttum 39220* (SING). Maturata, 1871, *Robinson* (K). Namunakula, *Freeman 10A* (BM). Same locality, 1950 m, 24 Feb. 1954, *Sledge 1200* (BM). *Ferguson* (PDA). *Wall* (K).

In forests on the higher mountains above 1800 m.

Nepal, Bhutan, Assam, S. China, Burma, Vietnam, Sumatra, Java, Borneo, New Guinea, Philippines.

The generic separation of *Diacalpe* and *Peranema* has hinged upon their sessile and pedicellate sori respectively. As mentioned below (p. 22) I have seen specimens of *Dryopteris gracillima* in which the sori are elevated on stalks as prominent as those of *Peranema cyatheoides*. Bower (*Ferns* 3 : 110 (1928)) attached more importance to the fact that in *Peranema* the indusium originates unilaterally, as in *Dryopteris*. But as the sorus develops the margins of the indusium grow forward so as to surround the base of the receptacle leaving only a very narrow slit on the distal side.

Illustrations of mature sori all show a complete ring of indusial tissue surrounding the base of the receptacle, and this I can confirm from my own dissections. So, although the early stages of development of the indusium may be dissimilar in the two, the final condition is virtually identical. In view therefore of the very close similarity of *Diacalpe* and *Peranema* not only in habit and frond morphology but also, as shown by Nayar and Kaur (*Bull. natn. bot. Gdns* Lucknow, 81 (1963)), in anatomy, spore characters and gametophyte generations, it seems evident that the traditional distinction between the two based on the sessile versus the stalked sori should properly be regarded as a specific rather than a generic difference.

Peranema aspidioides is a rare fern in Ceylon, limited to forests on the most elevated mountains. It has not been recorded from the mountains of southern India. Himalayan specimens reach a considerably larger size than those of Ceylon.

2. ***DRYOPTERIS*** Adans.

DRYOPTERIS Adans., Fam. Pl. 2 : 20, 551 (1763).

Rhizome erect, scales usually entire, sometimes lacerate or with glandular margins ; fronds pinnate to decompound, nearly always catadromic, narrow in outline or broadly based, with or without basiscopically enlarged lower pinnae, and with the pinnules or their segments bluntly or, less commonly, sharply serrate ; texture usually herbaceous ; indusia reniform.

The Ceylon species of *Dryopteris* are distinguished from those of *Polystichum* and *Arachniodes* by the combined characteristics of : erect rhizome, non-coriaceous fronds, reniform indusia.

The catadromic frond architecture which is so typical of *Dryopteris* species with bipinnate or decompound fronds is not a constant feature of the Ceylon species ; indeed three species, *D. ambigua*, *D. deparioides* and *D. obtusissima*, regularly have anadromic fronds. A fourth species, *D. simulans*, normally has opposite pinnules but when not opposite the sequence is anadromic. All belong however in my opinion unquestionably to *Dryopteris*. Both Ching and Copeland gave undue importance to anadromic frond architecture as a primary distinction of *Polystichum* and '*Rumohra*' from *Dryopteris*. By attaching an overriding importance to this single character Ching transferred to *Rumohra* species which are in all other respects wholly typical of *Dryopteris*. Amongst Ceylon ferns such an example is *D. obtusissima*, which Beddome and his contemporaries had all treated as only varietally distinct from *D. sparsa*. Nor was Ching consistent in this matter, for though he also saw specimens of *D. simulans* and *D. deparioides* and noted that the latter, like *D. obtusissima*, had anadromic fronds and on that account 'may as well be justified by inclusion in the same group' (*Sinensia, Shangai* 5 : 31 (1934)) he did not in fact include it.

It has to be recognized that occasionally in species of *Dryopteris* the arrangement of the pinnules and their venation departs from the normal catadromic plan, just as occasional species have a wide-creeping rhizome (e.g. *D. angustifrons* (Moore) Kuntze), or coriaceous fronds (e.g. *D. varia* (L.) Kuntze) or sharply spinulose-serrate pinnules (e.g. *D. dilatata* (Hoffm.) A. Gray). The generic transfer of a species on account of any one of these exceptional characteristics, when unsupported by other morphological reasons for doing so, is just as unnatural as to remove from the genus *Tectaria* those occasional species in which the veins are free instead of anastomosing. At the specific level too, though an anadromic or catadromic sequence of pinnules is normally constant in any one species, it is not invariably so. In *D. obtusissima* both arrangements may sometimes be observed even in a single frond.

Of the ten species, only *D. hirtipes*, *D. wallichiana* and *D. sparsa* are widespread beyond Ceylon. *D. pulvinulifera* occurs also in northern India though not in southern India. *D. approximata* and *D. deparioides* are confined to Ceylon and south India and the remaining species, with the possible exception of *D. gracillima*, are all endemic.

Key to Species of *DRYOPTERIS*

Fronds pinnate, pinnae lobed or deeply pinnatifid :
Lamina large :
Pinnae shallowly lobed . . . . 1. *D. hirtipes*
Pinnae deeply pinnatifid . . . . 2. *D. wallichiana*
Lamina small . . . . 8. *D. gracillima*
Fronds bipinnate to tripinnate :
Base of stipe densely scaly :
Axils of shortly stalked pinnae with black scales . . 3. *D. pulvinulifera*
Axils of subsessile pinnae without black scales . . 4. *D. approximata*
Base of stipe not densely scaly :
Lowermost pinnae basiscopically enlarged :
Pinnae stalked, basal basiscopic pinnule of lowermost pinnae enlarged :
Pinnules of middle pinnae ± 5 mm broad and 3–4 times as long, lowest pair opposite or basiscopic one nearer the axis . . 5. *D. sparsa*
Pinnules of middle pinnae ± 10 mm broad and 2–3 times as long, lowest pair with acroscopic one nearer the axis . . 6. *D. obtusissima*
Pinnae subsessile basal basiscopic pinnule of lowermost pinnae shortened 7. *D. simulans*
Lowermost pinnae not basiscopically enlarged :
Sori medial ; fronds 2–12 cm broad, minutely glandular . 8. *D. gracillima*
Sori marginal or intramarginal :
Lamina narrow, 3–8 cm broad . . 8b. *D. gracillima* var. *prolongata*
Lamina 8–35 cm broad :
Rhachis scaly at least in pinna axils :
Eglandular, stipes 40–60 cm long, lamina more than 20 cm broad 7. *D. simulans*
Glandular, stipes up to 20 cm long, lamina up to 20 cm broad 9. *D. ambigua*
Rhachis smooth . . . . 10. *D. deparioides*

1. **Dryopteris hirtipes** (Blume) Kuntze, Rev. Gen. Pl. 2 : 813 (1891).

Aspidium hirtipes Blume, Enum. Pl. Jav. : 148 (1828).
Aspidium atratum Wall., Numer. List : no. 380 (1829), *nom. nud.*

Aspidium atratum Wall. ex Kunze in Linnaea 24 : 279 (1851).

Nephrodium hirtipes (Blume) Hook., Sp. Fil. 4 : 115, t. 249 (1862).—C. B. Clarke in Trans. Linn. Soc. Lond., Ser. 2, Bot. 1 : 513 (1880).—Hope in J. Bombay nat. Hist. Soc. 14 : 721 (1903).

Polypodium scottii Bedd., Ferns Brit. Ind. : t. 345 (1870).

Dryopteris hirtipes var. *atrata* (Wall. ex Kunze) C. Chr. in Contr. U.S. natn. Herb. 26 : 278 (1931).

Dryopteris scottii (Bedd.) Ching apud C. Chr. in Bull. Dept. Biol. Coll. Sci. Sun Yatsen Univ. 6 : 3 (1933).

Dryopteris atrata (Wall. ex Kunze) Ching in Sinensia, Shanghai 3 : 326 (1933) ; in Bull. Fan meml Inst. Biol., Bot. 8 : 410 (1938), excl. syn. *Nephrodium gamblei* Hope.

Rhizome erect, scaly ; fronds tufted, up to 1 m long. Stipes about equalling the lamina, densely clothed at the base with dark brown, lanceolate, attenuate scales, 10–15 mm long, 2–3 mm wide ; elsewhere, like the rhachis, furnished with smaller and narrower, dark brown or black scales with sparsely toothed margins. *Lamina* oblong in outline and gradually attenuated upwards, up to 50 cm long and 30 cm broad, *pinnate with 10–20 pairs* of patent, oblong, acuminate *pinnae* below the pinnatifid apex ; *pinnae* sessile or subsessile, up to 15 cm long and 2 cm broad, gradually narrowed to the attenuate apex, base equal, rounded or truncate, very shortly stalked, *margins shallowly lobed* with broad, rounded, subfalcate lobes, veins in pinnate groups in the segments, simple or undivided, the basal pair stopping short well within the margin ; upper surfaces glabrous, lower surfaces with a few fibrils on the costa and veins ; texture herbaceous. Sori dorsal on the veins, commonly 2–4, rarely up to 6 to each group of veins, forming 2–3 irregular rows parallel to the costa and not extending into the lobes ; indusium small, round-reniform, fugacious.

CEYLON : Nuwara Eliya, Sept. 1844, *Gardner 1091* (CGE). Same locality, *Freeman 226A, 227B* (BM). Kandy, *Mrs Chevalier* (BM). Kotmalee, 1847, *Fortescue* (CGE). Hakgala, 1650 m, 20 Feb. 1954, *Sledge 1158* (BM). Forest on Namunakula, 1920 m, 24 Feb. 1954, *Sledge 1190* (BM). *Gardner 1140* (BM ; K). *Gardner 1291* (K). *Thwaites C.P. 1291* (BM ; E). *Mrs Walker* (K). *Robinson 163* (K). *Gossett* (K). 1872, leg. *Randall, R. W. Rawson 3220* (BM). *Miers* (US *58136*). *Ferguson* (US *815353, 816414*). *Wall* (E).

Forests of the interior above 900 m.

South India (Nilgiri, Anamallay and Pulney Hills), Himalayan region from Kashmir to Assam, Tibet, S. China, Burma, Thailand, Java, Borneo, Philippines, Formosa, Samoa.

According to Ching, Himalayan plants formerly referred to this species are not conspecific but constitute a separate species, *D. atrata*. A re-examination of Ching's treatment of these species and the abundant material available at Kew and the British Museum leaves me sceptical however of the soundness of his conclusions. I have failed to find any firm and constant characters which will serve to distinguish Wallich's *A. atratum* from Ceylon or South Indian plants. My Samoan specimens of *D. hirtipes*, which do not differ appreciably from Indian plants, have coal-black, non-fimbriate scales (or at most with occasional fimbriations) and thus combine two characters whereby Ching distinguished *D. atrata* from *D. hirtipes*. But both black scales and fimbriate scales can be seen on some South Indian and Ceylon plants. Kunze moreover, who first validated Wallich's name, based his description on six Nilgiri gatherings ; yet Ching omits mention of this area in the geographical range which he attributes to *D. atrata* and states that in India the latter is northern and *D. hirtipes* southern in distribution. Since his monographic account appeared it has been customary to use the name *D. atrata* for plants from the Himalayan region and *D. hirtipes* for plants from Southern India and Ceylon. Though I am not directly concerned with north Indian plants it is my belief that two species occur in the Himalayan region, viz. *D. hirtipes* and *D. gamblei* (Hope) C. Chr. and that Ching has confused rather than clarified the treatment of this group by wrongly uniting the distinct species *D. gamblei* with *D. atrata* and by wrongly separating *D. atrata* from *D. hirtipes*, with which it is, in my opinion, conspecific.

I am similarly unable to agree with Ching in treating Beddome's *Polypodium scottii* as a distinct species. Beddome himself concluded (*Suppl. Ferns Brit. Ind.* : 82 (1892)) that it was 'probably only an exinvolucrate variety of *Lastrea hirtipes*' and with this conclusion I am fully in agreement. The other differences ascribed by Ching to *D. scottii* do not appear to me to show any constant correlation with exindusiate sori, but to overlap completely with indusiate plants. Ching attributes a northern distribution to *D. scottii* but there are four sheets of *D. hirtipes* from Ceylon in Herb. Kew which are exindusiate as are some of the South Indian specimens. Christensen also refers (in *Gdns' Bull. Straits Settl.* 7 : 250 (1934)) to an exindusiate specimen from Borneo and there are five other exindusiate examples from there in the *D. hirtipes* cover at Kew. I have a frond of *D. hirtipes* from Ceylon in which no trace of indusium is to be seen on the young sori though other fronds from the *same population* of plants show indusia. Such plants were named *Nephrodium hirtipes* var. *exindusiata* by Clarke and if they deserve nomenclatural recognition this, rather than the specific level, seems the appropriate grade to accord to them.

Dryopteris hirtipes is easily distinguished from all other Ceylon species of *Dryopteris* by its simply pinnate fronds with shallowly lobed pinnae. Thwaites and Wall both stated that it was a common species in the higher forests of the interior but that has not been my experience.

2. ***Dryopteris wallichiana*** (Spreng.) Hyl. in Bot. Notiser 1953 : 352 (1953).

Aspidium paleaceum sensu D. Don, Prodr. Fl. Nepal. : 4 (1825), non Swartz.
Aspidium wallichianum Spreng. in L., Syst. Veg. ed. 16, 4(1) : 104 (1827).
Aspidium donianum Spreng., op. cit. 4(2) : 320 (1827), *nom. superfl.*
Aspidium patentissimum Wall., Numer. List : no. 340 (1829), *nom. nud.*
Lastrea patentissima C. Presl, Tent. Pterid. : 76 (1836), *nom. nud.*
Dichasium patentissimum Fée, Mém. Fam. Foug. 5 : 302 (1852), *nom. nud.*
Nephrodium filix-mas var. *paleaceum* Hook., Fil. Exot. : t. 98 [delin. a specim. ex Ceylon] (1859) pro parte, non *Lastrea filix-mas* var. *paleacea* T. Moore.
Lastrea patentissima Bedd., Ferns S. Ind. : 39, t. 111 (1864), *nom. superfl.*
Nephrodium filix-mas var. *patentissimum* C. B. Clarke in Trans. Linn. Soc. Lond., Ser. 2, Bot. 1 : 520 (1880).

Lastrea filix-mas var. *parallelogramma* Bedd., Handb. Ferns Brit. Ind. : 249 (1883) pro parte, non *Aspidium parallelogrammum* Kunze.

Dryopteris filix-mas subsp. *patentissima* (C. B. Clarke) C. Chr., Index Fil. : 265 (1905), excl. *Nephrodium filix-mas* var. *fibrillosum* C. B. Clarke.

Dryopteris paleaceum Hand.-Mazz. in Verh. zool-bot. Ges. Wien 58 : (100) (1908), *nom. superfl.*—Ching in Bull. Fan meml Inst. Biol., Bot. 8 : 427 (1938), excl. parte.

Dryopteris doniana Ching in Sunyatsenia 6 : 3 (1941), *nom. superfl.*

Rhizome erect, bulky ; fronds tufted, up to 1·5 m long. Stipes shorter than the laminas, up to 40 cm long, stout, densely clothed at the base with long, narrow, lanceolate, attenuate, entire, dark brown scales, often with black striae, up to 3 cm in length, elsewhere, like the rhachis, furnished with narrower, linear to filiform, finely pointed, entire, chestnut to black scales. *Lamina* 50–100 × 20–40 cm, oblong in outline, narrowed above, *pinnate with 20–40 pairs of* patent, oblong, acuminate, *deeply pinnatifid pinnae* ; pinnae subsessile, 10–20 × 2–3 cm gradually narrowed to the attenuate apex, the lowermost not or scarcely reduced, divided almost to the costa into oblong segments about 5 mm broad with parallel sides and broadly rounded to truncate, obscurely denticulate apices, veins pinnate in the segments, forked, both surfaces fibrillose on the costa, texture firmly herbaceous. Sori forming two rows in the segments, dorsal on the acroscopic branch veins and closer to the midrib than to the margin ; indusium small, orbicular, more or less persistent.

CEYLON : *Thwaites C.P. 1364* (BM ; E ; K ; PDA, Nuwara Eliya, Jan. 1847, Apr. 1856, *Gardner*). Nuwara Eliya, *Freeman 242A, 243B* (BM). Between Hakgala and Sita Eliya, 30 June 1927, *J. M. de Silva* (PDA). By path from Pattipola to Horton Plains, 1950 m, 20 Dec. 1950, *Sledge 674* (BM). Jungle at Horton Plains, 2100 m, 20 Dec. 1950, *Sledge 677* (BM). Same locality, 2270 m, 7–8 March 1954, *Schmid 1399* (BM). Adam's Peak, *Moon* (BM). Same locality, 2190 m, 14 Feb. 1908, *Matthew* (K). *Ferguson* (US *816412*). *Hooker f. & Thomson 256* (BM). *Robinson 164* (K). Hort. Kew ex Ceylon, 1857, 1858 ex *Herb. J. Smith* (BM). *Wall* (GL ; E). *Wight 1942* (E).

Forests of the most elevated parts of the interior, above 1900 m.

South India (Nilgiri Hills), Himalayan region from Simla to Assam, Yunnan, Burma, Java, Borneo (Kinabalu), New Guinea, Philippines, Formosa.

I follow others in treating Asiatic plants as distinct from Swartz's Peruvian *Aspidium paleaceum.* Of the many names which have been given to the Indian plant the oldest valid one is Sprengel's, who first called it *Aspidium wallichianum* but changed the name to *A. donianum* in the second part of the same volume on account of there already being an *A. wallichii* Hook. Since it is stated on the last page of the first part that corrections and additions would soon be published one must assume that the two parts were not issued simultaneously and hence the corrected name must be taken as later and superfluous.

Dryopteris wallichiana is readily distinguished from *D. hirtipes* by its deeply pinnatifid or subbipinnate fronds. It is a rarer species in Ceylon and all localized specimens come from the Nuwara Eliya or Adam's Peak areas, though it is likely to be present elsewhere at sufficiently high elevations. *D. wallichiana* resembles the

European *D. pseudo-mas* (Wollast.) Holub (= *D. borreri* Newm.) and is an apogamous triploid as is commonly the case with the latter.

3. ***Dryopteris pulvinulifera*** (Bedd.) Kuntze, Rev. Gen. Pl. 2 : 813 (1891).—Ching in Bull. Fan meml Inst. Biol., Bot. 8 : 466 (1938).

Lastrea pulvinulifera Bedd., Ferns Brit. Ind. : t. 333 (1870) ; Handb. Ferns Brit. Ind. : 255 (1883).
Nephrodium pulvinulifera (Bedd.) Bak. in Hook. & Bak., Synops. Fil., ed. 2 : 500 (1874).
Lastrea pulvinulifera var. *zeylanica* Bedd., Suppl. Ferns S. Ind. & Brit. Ind. : 17 (1876).
Nephrodium sparsum var. *squamulosum* C. B. Clarke in Trans. Linn. Soc. Lond., Ser. 2, Bot. 1 : 524 (1880).
Lastrea sparsa var. *zeylanica* (Bedd.) Bedd., Handb. Ferns Brit. Ind. : 254 (1883).

Rhizome erect, its apex and the bases of the tufted stipes clothed with a *dense cushion-like mass of linear, dark ferruginous scales* 2 cm long ; *stipe and rhachides*, both primary and secondary, furnished *with narrow black scales especially in the axils of the pinnae.* Fronds up to 75 cm long, 30 cm broad, deltoid, tripinnate, the pinnae very shortly stalked, lowermost opposite and largest or at least not reduced and not basiscopically enlarged ; pinnules up to 5 cm long on basal pinnae 'with their secondary pinnules equal to the primary pinnules on the upper parts of the frond', the lower ones with subacute apex and pinnate, the segments with subentire margins and serrate apices, the upper ones obtuse with dentate margins, pinnule rhachis and costas bearing black scales beneath and *both surfaces of the lamina furnished with short, cylindrical, shining, white hairs.* Sori terminal on acroscopic branch veins, about equidistant from costule and margin of segment. Indusium thin, brown.

CEYLON : *Thwaites C.P. 4007*, Central Province, 1869, and Blackpool, Nuwara Eliya, comm. *Wall* (PDA). Blackpool, *Wall* (K). Same locality, *Freeman 250A, 251B* (BM). Tonacombe, Uva Province, *Freeman 252A* (BM). Adam's Peak, *Moon* (BM). Same locality, 2100 m, 14 Feb. 1908, *Matthew* (K). Hakgala, 2 Sept. 1926 ?, as *Athyrium macrocarpum* (PDA). Horton Plains, 2270 m, 7–8 March 1954, *Schmid 1389* (BM). Above track from Ramboda Pass to Maturata, amongst rocks near stream in forest, 1920 m, 17 March 1954, *Sledge 1295* (BM ; K). *Hance 1079*, coll. *Bradford* (BM).

Forests in the higher parts of the interior.

Sikkim, Khasia.

The dense *Hypodematium*-like cushion of basal scales and the black scales of the rhachis and pinna rhachis and especially in the axils of the pinnae make this a well-marked species quite distinct from *Dryopteris sparsa* and its allies. In addition the distinctive short, blunt, shining hairs on the lamina – referred to as setae by Beddome – are alone sufficient to separate it from all other Ceylon species.

Beddome had evidently seen very little Ceylon material when he described plants from there as a distinct variety, for the characters attributed to Ceylon plants are not generally applicable. There are also very small plants from Khasia with fertile fronds less than 10 cm long at Kew. His later transference of the variety from

D. pulvinulifera to *D. sparsa* was still less reasonable. I agree with Ching (loc. cit.) that Ceylon plants do not differ significantly from North Indian ones.

Dryopteris pulvinulifera is one of a group of ferns – of which *Microsorum dilatatum* (Bedd.) Sledge, *Prosaptia khasiana* (Hook.) C. Chr. and Tard. and *Microlepia firma* Mett. ex Kuhn are other examples – occurring in North India and Ceylon but absent from southern India.

4. ***Dryopteris approximata*** Sledge, sp. nov. (Text-fig. 1.)

Ex affinitate *D. ramosa* sed differt paleis marginibus irregulariter dentatis fimbriatisque, pinnis sessilibus vel paene sessilibus, pinnulis segmentis minus profunde acutisque dentatis, indusiis valde convexis, magis perdurantibus.

Rhizoma *basesque stipitum caespitosorum dense vestitae paleis tenuibus lanceolatis vel linearibus ferrugineo-brunneis, subtiliter acutis, marginibus irregulariter dentatis*

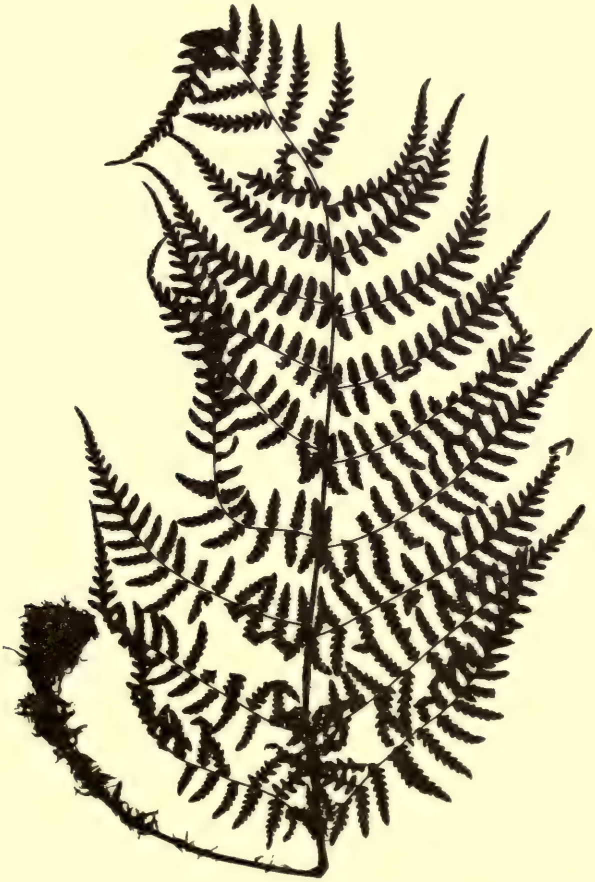

FIG. 1. *Dryopteris approximata* Sledge. Frond (*C.P. 1375*, Herb. PDA). × ⅓.

fimbriatisque 1·0–2·5 cm longis. Frondes usque ad 1 m longae ; stipites 20–30 cm straminii infime squamati sursum glabrescens ; rhachis juventute paleis perangustis dentatis fibrillisque sparsim vestita quae plerumque circum bases pinnarum persistunt. Lamina ovata 30–60 × 20–30 cm, bipinnata pinnulis pinnatifidis vel in frondibus amplis basi subtripinnata, infra non angustata ; *pinnae* remotae *sessiles vel paene sessiles paribus basalibus pinnularum rhachi approximatis* et saepe quam sequentes brevioribus, inferiores usque ad 30 cm longae, 4–7 cm latae, gradatim decrescentes, *pinnulae in lateribus basiscopis pinnarum inferiorum non vel non nisi parum dilatatae* ; pinnulae bene disparatae, oblongae, acutae vel acuminatae hae mediarum pinnarum 1·5–2·5 cm longae sed interdum usque ad 6 cm in pinnis infimis, adnatae, basibus posticis decurrentibus in ala pinnae rhachidis marginibusque serratis in parte superna frondis, lobatescentes tum leviter usque profunde pinnatifidae in parte inferiore, basibus sessilibus subsessilibusve aequalibus, segmentis dentatis, utrinque glabratae praeter fibrillas paucas infra in venis ; textura chartacea. Sori in uno quoque lobo singuli, mediales in vena acroscopica ; indusia firma, valde convexa, perdurantia. Sporae plano-convexae, verrucosae.

CEYLON : *Thwaites C.P. 1375*, Central Province, 1861 (BM ; CGE ; E ; K ; PDA holotype). Hort. Kew [ex Namunakula, 1800–1900 m, 24 Feb. 1954, *T. G. Walker 571*] *Alston 17505* (BM). In forest on Namunakula, 1875 m, 24 Feb. 1954, *Sledge 1201* (BM). Madulsenia, *Wall* (K). 1884, *Wall* (PDA). 1864, *Gower Coll.* (E). *Ferguson* (US *816439* partim).

SOUTH INDIA : Courtallum, Aug. 1835, *Wight 186* (K). Lambs rock shola, 1800 m, June 1883, *Gamble 11790* (K). Same locality, Sept. 1883, *Gamble 12407* (K). Periya shola, Pulneys, 21 April 1898, *Bourne 4920* (K). Same locality, 18 June 1898, *Bourne 4921* (K). Perumbukanal, Pulneys, 21 May 1898, *Bourne 4922* (K). Same locality, 21 June 1898, *Bourne 4925, 4926* (K). Nilgiris, *Beddome 127, 127B* (K). Pulney Hills, 1680 m, *Saulière 443* (K). Coolie path near Shembag, Pulney Hills, c. 1800 m, May 1936, *Arokiasamy 31* (BM).

Dryopteris approximata is at once distinguished from *D. sparsa* and *D. obtusissima* by the densely scaly bases of its stipes, by its sessile pinnae, by the basiscopic pinnules of the lower pinnae not being enlarged and by its more symmetrical pinnules, not unequal at their bases. Thwaites's Ceylon specimens are named *Nephrodium sparsum* ; the South Indian specimens are mostly named *N. filix-mas* var. *elongatum*. Most of the older Indian collections to which the latter name was applied are *D. marginata*, but later Hope described another species, *Nephrodium ramosum*, from the north-western Himalayas, which ranges from Simla to Kashmir and Afghanistan and the present fern is very much closer to this. It may be a geographical subspecies of *D. ramosa* ; Ceylon and South Indian specimens however are notably uniform and none exactly match any of the Himalayan plants. It differs from these in its toothed and fimbriate scales, its less sharply and less deeply toothed pinnule segments and in its larger sori with darker brown, thicker, strongly convex and more persistent indusia. Both species have the basal pinnules lying near to the frond axis, but in *D. ramosa* the pinnae are very shortly stalked – up to 5 mm – whereas in *D. approximata* the stalks are at most 1–2 mm long. Hope also states that in *D. ramosa* the

pinnules of the lower pinnae are 'much longest on the lower side' which is not the case in Ceylon and South Indian plants.

The name applies equally to the closeness of the pinnules to the frond axis and of the species to *D. ramosa*.

This is evidently a rarer species in Ceylon than in S. India. Thwaites took it to be the true *D. sparsa* and distributed many specimens so named. There are four sheets of it as *C.P. 1375* in Herb. Peradeniya (and two others of Wall's named *Lastrea filix-mas* var. *elongata* Hk. & Grev., var. *marginata* Moore). Yet the commoner *D. sparsa* is represented in Herb. Peradeniya by two sheets only.

5. ***Dryopteris sparsa*** (D. Don) Kuntze, Rev. Gen. Pl. 2 : 813 (1891).

Nephrodium sparsum D. Don, Prodr. Fl. Nepal. : 6 (1825).
Aspidium sparsum (D. Don) Spreng. in L., Syst. Veg., ed. 16, 4(1) : 106 (1827).
Nephrodium purpurascens Hook., Sp. Fil. 4 : 132, t. 262 (1862) pro parte, non *Aspidium purpurascens* Blume.
Lastrea sparsa (D. Don) Bedd., Ferns S. Ind. : 36, t. 103 (1863) excl. parte ; Handb. Ferns Brit. Ind. : 252 (1883) excl. parte.
Nephrodium sparsum var. *latisquamum* C. B. Clarke in Trans. Linn. Soc. Lond., Ser. 2, Bot. 1 : 524 (1880).

Rhizome covered with broad, thin, brown scales with acute apices and entire or subentire margins. Fronds up to 1 m long but often smaller. Stipes 20–40 (50) cm, lower part dark brown, stramineous above, scaly, the scales similar to those of the rhizome ; *rhachis* without scales but *bearing* numerous very short clavate to globose unicellular *papillae in the dorsal groove* especially about the junction with the pinna rhachides, which are similarly papillate above in the proximal part. Lamina 20–40 (50) × 8–25 cm, bipinnate or tripinnatifid below in large fronds, oblong-lanceolate to narrowly deltoid-ovate in outline, *catadromic* ; *pinnae* well spaced, shortly stalked, the lowermost pair with the *basiscopic basal pinnules always somewhat longer and usually conspicuously longer than the rest*, commonly 3–5 cm long and incised or pinnatifid, in large fronds up to 8 cm long and pinnate ; pinnules of middle pinnae three to four times as long as broad, mostly about 5 mm broad with blunt apices, unequal at the base with the posterior margin decurrent on the rhachis, the margins shallowly lobed with a short sharp tooth above the sinus on the anterior margin of each lobe, glabrous on both surfaces, texture stiff-herbaceous. Sori mostly one to each lobe, medial on the acroscopic vein ; indusia firm, papillate, persistent. Spores monolate, 45–55 × 27–33 μm, broadly winged and with anastomosing surface ridges.

CEYLON : Nuwara Eliya, 1871, *Robinson* (K). Same locality, *Freeman 244A* (BM). Oodawella, *Hutchinson 70* (BM). Midford, Ambagamuwa District, 1200 m, 29 Jan. 1954, *Sledge 1062* (BM). Roadside bank between Duckwari and Rangalla, 7 Jan. 1951, *Ballard 1423* (K). Shady bank by roadside, Rangalla, 1050 m, 30 Jan. 1954, *Sledge 1091* (BM). Le Vallon, 9 Feb. 1954, *Sledge 1103* (BM). Namunakula, 1875 m, 24 Feb. 1954, *Sledge 1201B* (BM). Tangamalai Sanctuary, Haputale, 1500 m, 25 Feb. 1954, *Sledge 1206* (BM). Amongst rocks near stream in forest above path from Ramboda Pass to Maturata, 1920 m, 17 March 1954, *Sledge 1296* (BM).

Gardner 1148 (BM). *Thwaites C.P. 1368* (BM). *Thwaites C.P. 1369* pro parte (PDA). *Thwaites C.P. 1375* pro parte (K). *Ferguson* (US *816438* pro parte). *Wall* (E).

Mountain forests above 1000 m.

South and North India, China, Burma, Thailand, Malaya, Java, New Guinea, Philippines, Formosa, S. Japan.

Much confusion has surrounded the identity of *Dryopteris sparsa* in Ceylon. Under *Aspidium sparsum* five C.P. numbers are cited by Thwaites (*Enum. Pl. Zeyl.* : 392 (1864)). These five numbers represent five different species not one of which is *D. sparsa*. Another quite distinct species was later added to this heterogeneous collection under the name var. *zeylanica*.

Wall's understanding of these ferns, based on his intimate field knowledge of them, is well shown in his comments (*Cat. Ferns Indig. Ceylon* : 5–6 (1873)) upon the supposed variability of *D. sparsa* where he expressed the view that 'It appears, however, to contain several distinct types, not fully connected together, and which it would be convenient to distinguish under separate names'. He then clearly distinguished between true *D. sparsa*, as represented by Hooker's (loc. cit.) figure of *Nephrodium purpurascens* and *D. simulans*, *D. pulvinulifera* and *D. obtusissima* which 'though subject to such variations as are common to all species, do not appear to be so connected by intermediate links as at any time to lose their distinctive characters'. He also refers to 'yet another form, of which I have seen only three specimens ; but as they are extremely small, it may be that they are stunted and abnormal'. This was *D. gracillima*. He thus recognized all five of the species which were included by Thwaites within *D. sparsa* and his acumen was further demonstrated by his rejection (vide infra p. 17) of *Aspidium undulatum* Thwaites as a distinct species.

Of the five sheets of *C.P. 1375* at Peradeniya cited in *Enum. Pl. Zeyl.* as typical *Aspidium sparsum*, four are *Dryopteris approximata* and one *D. obtusissima*. Apart from one relatively recent addition to the collection there is only a single sheet of true *D. sparsa* in the Peradeniya Herbarium. Ceylon specimens are not numerous in other herbaria and it is evidently less common there than *D. obtusissima* although I made about the same number of collections of each species.

Beddome's illustration (*Ferns S. Ind.* : t. 103 (1863)) is uncharacteristic and inaccurate. Though the accompanying description refers to the pinnules as having 'rounded obtuse entire lobes' the drawing shows them with sharply acuminate teeth. I suspect that, like Thwaites, he did not clearly distinguish *D. sparsa* from other species. The description in the *Handbook* seems clearly to be compounded of more than one species since he refers to the rhizome as being 'densely covered with lanceolate-linear golden or reddish scales' and the pinnules as 'often quite sharply serrated'. Neither of these characters is applicable to true *D. sparsa*.

6. ***Dryopteris obtusissima*** (Mett.) Christ in J. Bot. Paris, Ser. 2, 1 : 231 (1908).

Aspidium undulatum Thwaites, Enum. Pl. Zeyl. : 444 (1864 sero), *nom. monstr.*, non *A. undulatum* Afzel. (1801).

Lastrea undulata Bedd., Ferns S. Ind. : 88, t. 271 (Sept. 1864), *nom. monstr.*
Nephrodium undulatum Bak. in Hook. & Bak., Synops. Fil. : 276 (1867), *nom. monstr.*
Aspidium obtusissimum Mett. apud Kuhn in Linnaea 36 : 119 (1869).
Lastrea sparsa var. *obtusissima* (Mett.) Bedd., Suppl. Ferns S. Ind. & Brit. Ind. : 17, t. 375 (1876) ; Handb. Ferns Brit. Ind. : 254, fig. 131 (1883).
Lastrea sparsa var. *undulata* Bedd., Handb. Ferns Brit. Ind. : 254 (1883) *nom. monstr.*
Dryopteris undulata Kuntze, Rev. Gen. Pl. 2 : 814 (1891), *nom. monstr.*
Rumohra obtusissima (Mett.) Ching in Sinensia, Shanghai 5 : 62 (1934).
Rumohra zeylanica Ching, tom. cit. : 70 (1934), *nom. monstr.*
Arachniodes obtusissima (Mett.) Ching in Acta bot. sin. 10 : 259 (1962).
Arachniodes zeylanica Ching, tom. cit. : 260 (1962), *nom. monstr.*

Rhizome clothed with broad, brown, entire, acute scales, 5–10 mm long. Fronds 40–80 (100) × 15–30 cm. Stipes up to 40 cm, scaly, the scales similar to but somewhat narrower than those of the rhizome ; rhachis usually with a few narrow scales especially about the points of attachment of the pinnae, *papillate in the dorsal groove* about the junction with the pinna rhachides, which are similarly papillate above. Lamina about as long as the stipe, bipinnate or tripinnate, ovate to rhombic-ovate in outline ; *pinnae* spaced, *stalked, anadromic,* the lowest pair with the basiscopic pinnules enlarged, 10–20 (30) cm long with the longest pinnules usually 3–6 cm long but up to 12 cm in large fronds ; basal pinnules shortly stalked, becoming sessile then adnate and unequal at the base with the posterior margin decurrent on the rhachis, the anterior margin often subauriculate, *those of the middle pinnae two or three times as long as broad, mostly about 1 cm broad with rounded obtuse apices* but often subacute or acute in large fronds and even attenuate, sub-entire, crenate-lobate or pinnatifid with toothed lobes or the lower pinnae fully pinnate in large fronds with the ultimate segments blunt and sub-entire or serrate, both surfaces glabrous, texture firm-herbaceous. Sori mostly one to each lobe in the smaller pinnules and nearer the margin than the costa or in two rows on the segments of the larger divided pinnules ; indusia thin, papillate, not persistent. Spores monolete, 42–51 × 27–33 μm, with a broad undulate perispore wing and dense irregular surface ridges.

CEYLON : *Thwaites C.P. 1369* (BM ; CGE ; E ; K ; PDA). *Thwaites C.P. 1368,* pro parte (E ; K). *Gardner 1097* (BM ; CGE, in woods, Nuwara Eliya, June 1845 ; K). Nuwara Eliya, 1820 m, 10 May 1906, *Matthew* (K). Same locality, July 1887, no collector's name (E). Same locality, *Freeman 245B, 246C, 247D, 248E, 249F* (BM). Kandapola near Nuwara Eliya, 1800 m, 19 March 1954, *Sledge 1328* (BM ; US). Hakgala, 1871, *Robinson* (K). Same locality, 1650 m, 23 Dec. 1950, *Holttum 39155* (SING). Horton Plains, 2100 m, 19 Dec. 1950, *Sledge 690* (BM ; US). Same locality, 2270 m, 7–8 March 1954, *Schmid 1374* (BM). Knuckles Mt., 1650 m, 30 Jan. 1954, *Sledge 1083* (BM). Adam's Peak, 14 Feb. 1908, *Matthew* (K). Same locality, 1650–1950 m, 14 Dec. 1950, *Sledge 607, 617, 623* (BM). Jelumalai, Namunakula, 12 March 1907, *J. M. Silva* (PDA). Namunakula, 1920 m, 24 Feb. 1954, *Sledge 1186* (BM). 12 March 1819, *Moon 470* (BM). *Gardner 1253,* pro parte (K). 1899, *Anderson* (E). *Walker* (K). *Wight 1923, 1946* (E). *Wall* (E ; K ; PDA).

In mountain forests.

Endemic.

Dryopteris obtusissima varies much in size and dissection of the fronds. These are commonly bipinnate with broad, obtuse, shallowly lobed pinnules, but the largest fronds may attain a metre in length and be tripinnate with the lowest pinnae 20–30 cm long and with pinnules which may reach a length of 12 cm. In such large fronds the pinnules are invariably acute and may even be attenuated. The pinnule segments are then rounded and obtuse. Although extremes look very different it would serve no useful purpose to describe varieties based on the subdivision of the frond or shape of the pinnules since the boundaries between such varieties would be quite arbitrary on account of the intergrading forms which occur. Mettenius cited *Gardner 1097, 1253* and *Thwaites 1369*. Specimens of the first number in the type cover at Kew show two bipinnate fronds with blunt pinnules and one subtripinnate with acute pinnules. One of the BM sheets of the same number (ex Herb. John Smith) is the large-fronded, fully tripinnate form. Two of the three sheets of *Gardner 1253* at Kew carry fronds of both *D. obtusissima* and *D. simulans* ; the third is *D. simulans* as is also the Cambridge sheet of the same number.

Dryopteris obtusissima differs from *D. sparsa* in its shorter, broader and blunter pinnules, two to three times as long as broad in the former, three to four times in the latter. In *D. obtusissima* the basal acroscopic pinnule is usually situated nearer to the rhachis than is the basiscopic basal pinnule, i.e. the pinnules are anadromic. This arrangement of the pinnules is reversed in *D. sparsa* with the basiscopic ones nearer to the rhachis though often the basal pinnules are subopposite. In *D. obtusissima* both the basal basiscopic pinnules and the remaining ones on the lower side of the lowermost pinnae are enlarged, a gradual reduction in size taking place from proximal to distal end of the pinna. In *D. sparsa* the basal basiscopic pinnules of the lowermost pinnae are enlarged – usually conspicuously so – whilst the remaining pinnules are often little different in size on the two sides of the pinna. Other differences are the presence of some scales especially near the axils of the pinnae, the supra-medial sori and the more delicate non-persistent indusia in *D. obtusissima* as contrasted with the smooth rhachis, medial sori and firm, strongly convex and persistent indusia in *D. sparsa*. The spores are also different in the two species, as described.

D. obtusissima is probably confined to Ceylon. It is not present in southern India and Clarke does not include it amongst the north Indian forms of *D. sparsa*. There is a single gathering at Kew, ex Herb. Beddome, collected by Jerdon and said to come from Sikkim Himalaya but the fronds have been remounted and I doubt if the label can be relied upon. I also conclude from Beddome's statement (*Suppl. Ferns Brit. Ind.* : 57, 1893) that 'Some of the North Indian varieties of the very variable *L. sparsa* var. *obtusissima* are very puzzling, and might as well be referred to *Filix-mas* as to *sparsa*', and his identification (op. cit. : 60) of *Clarke 36790* and *41639* from Sikkim and Kohima as *L. sparsa* var. *obtusissima*, neither of which gatherings belongs either to *D. sparsa* or to *D. obtusissima*, that he was not well acquainted with this species. Ching (in *Sinensia, Shanghai* 5 : 62 (1934)) also considered it endemic to Ceylon.

The abnormally developed plants named *Aspidium undulatum* by Thwaites (*Enum. Pl. Zeyl.* : 444 (1864)), the fronds of which have a strongly zig-zag rhachis, belong here. Their bizarre appearance has led to numerous collections being made and they are consequently well represented in herbaria. The most extreme examples, such as those on which Thwaites founded his species, are plainly teratological, and hence his name, and those based on it, must be rejected as founded on a monstrosity. The irregular cellular behaviour which gives rise to the abnormal zig-zag development of the rhachis could well be caused by a virus infection. Beddome illustrated such an extreme form (*Ferns S. Ind.* : 88, t. 271 (Sept. 1864)) as *Lastrea undulata* from a specimen sent to him by Thwaites. The frond depicted and others similar to it in herbaria bear little resemblance to *D. obtusissima* ; less extreme ones are nearly always tripinnate with much smaller pinnules and pinnule segments than in *D. obtusissima,* but intermediate conditions between the two are represented on herbarium sheets at Kew and Peradeniya. These varied states could well be an expression of varied degrees of pathogenicity. Although *A. undulatum* is said to have been discovered by W. N. Beckett at Wattakellie Hill – the type locality – in 1864, it had been collected by Gardner near the summit of Adam's Peak in March 1846. His specimen (*Gardner 1254,* CGE) plainly shows in its pinnule shape the relationship with *D. obtusissima.*

When Ching raised this fern to specific rank again as *Rumohra zeylanica,* he ignored the testimony of those familar with it in the field. Wall (*Cat. Ferns Indig. Ceyl.* : 6 (1873)) states that at Wattakellie Hill it 'occurs both with and without the undulate stipes and rachis which form its distinctive character'. He adds also that 'slightly undulate and perfectly normal fronds are often found on the same plant'. Ferguson (*Ceylon Ferns* : 39 (1880)) also states that at Wattakellie Hill the fronds of *Aspidium undulatum* 'so run into this one [*D. sparsa*], that I should suspect the flexuose rachis to be an abonormal [sic] state of this variable fern'. Ceylon botanists soon doubted the validity of *Aspidium undulatum* as a species and certainly in view of Wall's and Ferguson's observations it should not be given that rank, or indeed any systematic rank, for one cannot have two taxa on the same rhizome! I have not seen living plants of this fern. Its behaviour in cultivation would be a matter of interest, and experimental observations are necessary to determine the morphogenetic explanation of its abnormal growth.

The specimens of this abnormal form that I have seen are not listed above. They are :

CEYLON : *Thwaites C.P. 3858* (BM ; CGE ; E ; K ; PDA, from Wattakelle, Kallibokka, 1500 m, Sept. 1864, coll. *Beckett*). *Thwaites C.P. 1369,* pro parte (K, Bogawantalawa, 1500 m ; PDA). Near summit of Adam's Peak, March 1846, *Gardner 1254* (CGE). 'Type of tab. 271', Wattakelly Hill, 1500 m, ex *Herb. Beddome* (K). In profusion at about 1800 m in a damp hollow near the Wettanagala Peaks, 12–14 miles E.S.E. of Adam's Peak, 1890, *T. Farr* (PDA). Maskeliya, *Maclure* (PDA). Hakgala, in jungle, 22 Feb. 1927, *Alston 1028* (PDA). *Hance 11475* ex *Thwaites* (BM). *Wall* (BM ; E ; GL).

7. ***Dryopteris simulans*** Ching in Bull. Fan meml Inst. Biol., Bot. 8 : 473 (1938).

Lastrea deltoidea Bedd., Ferns S. Ind. : 83, t. 248 (1864), *non L. deltoidea* T. Moore (1858).
Lastrea sparsa var. *deltoidea* Bedd., Handb. Ferns Brit. Ind. : 254 (1883).

Rhizome covered with broad, thin, brown scales; fronds tufted, up to 1 m long. Stipes 40–60 cm bearing scattered, thin, pale-brown scales, upper part and rhachis smooth save about the axils of the pinnae; *dorsal groove of rhachis not papillate* but *scaly* at the junction with the pinna rhachides, and often along the adjacent part of the pinna rhachis. Lamina 30–40 × 25–35 cm, bipinnate with lobed or pinnatifid pinnules, sometimes tripinnate in large fronds, deltoid-ovate or oblong-deltoid in outline; *pinnae* distant, *patent, the lower ones opposite or nearly so, sessile or very shortly stalked with the basal pinnules lying close to* and often overlapping *the main rhachis,* the *lowermost pair with the basal basiscopic* and often the basal acroscopic *pinnule shortened*; pinnules oblong-ovate blunt with shallowly or deeply lobed margins, often with a sharp tooth above the sinus on the anterior margin of each lobe, those of the middle pinnae 1–2·5 × 0·5–1 cm, glabrous on both surfaces, texture firm-herbaceous. Sori mostly one to each lobe in the smaller pinnules and nearer the margin than the costa, or in two rows on the segments of the more divided lower pinnules; indusia thin, not persistent. Spores monolete 39–45 × 24–30 μm with a broad undulate perispore wing up to 9 μm wide and anastomosing surface folds.

CEYLON: *Thwaites C.P. 1368* (PDA). *Gardner 1253* pro parte (CGE, forests between Adam's Peak and Nuwara Eliya, March 1846; K, same locality and Kaduganawa, 600–900 m). Hoolankande, 1350 m, 20 Jan. 1954, *Sledge 1014* (BM). Gallebodde, 1050 m, 26 Jan. 1954, *Sledge 1044* (BM). Gallebodde Rock, 1140 m, 27 Jan. 1954, *Sledge 1058* (BM). Midford, 1200 m, 29 Jan. 1954, *Sledge 1061* (BM). *Beddome* (K). *Ferguson* (US *816417, 8, 9*). 17 Feb. 1819, *Moon 215* (BM). *Robinson 166, 167* (K). *Wall* (E). *Wight 1923, 1927* (E). *Walker* (K).

In mountain forests.

Endemic.

Dryopteris simulans is readily distinguished by its patent pinnae the lower pairs of which – and sometimes all but the uppermost – are opposite, and by the basal pinnules also being opposite and inserted so low down on the pinna rhachis that they stand alongside and often overlap the main rhachis. When, as is occasionally the case, they are not opposite, the arrangement is anadromic. It is also notably distinct in having the basal pinnules of the lowermost pinnae reduced in size in contrast to those of *D. sparsa* and *D. obtusissima* in which they are enlarged on the basiscopic side. The other pinnules on the basiscopic side of the lowermost pinnae are not or scarcely larger than the acroscopic ones. The presence of scales in and about the axils of the pinnae and the absence – or at most the very weak development – of papillae in the dorsal groove of the rhachis are other characteristic features.

D. simulans has not been found outside Ceylon. It is less common there than *D. sparsa* or *D. obtusissima* and apparently favours lower altitudes. My own gatherings are from elevations of 1050–1350 m and on one of the Kew sheets an altitude of 2000–3000 ft (600–900 m) is cited. *D. obtusissima* ranges from 1650 to 2270 m, and *D. sparsa* from 1050 to 1920 m.

8. **Dryopteris gracillima** Ching in Bull. Fan meml Inst. Biol., Bot. 8 : 452 (1938).

Nephrodium sparsum var. *minus* Thwaites ex Bak. in Hook. & Bak., Synops. Fil., ed. 2 : 498 (1874).

Lastrea sparsa var. *minor* (Thwaites ex Bak.) Bedd., Suppl. Ferns S. Ind. & Brit. Ind. : 17 (1876) ; Handb. Ferns Brit. Ind. : 254 (1883).

Rhizome decumbent or erect, clothed at the apex with narrow, acute, brown scales. Fronds tufted, very variable in size and outline, sometimes (var. *gracillima*) short with elliptic or lanceolate lamina, or (var. *prolongata*) tall with linear lamina up to eight times as long as broad, or (var. *triangularis*) with triangular lamina widest at the base and up to twice as long as broad, but *always studded with minute glands on the scales, stipe, rhachis and under surface of the lamina, especially near the attachment of the pinnae and pinnules.* Stipe bearing small, scattered, spreading, acute, brown scales. Lamina simply pinnate, subbipinnate or fully bipinnate with anadromic pinnules ; pinnae in simply pinnate forms with dentate or shallowly lobed margins, inferior base cuneate, superior base auriculate, becoming more deeply lobed in the lower pinnae, often with the basal acroscopic lobe free or sometimes with several free lobes ; in bipinnate forms with up to six pairs of toothed or lobed or even pinnatifid pinnules. Sori medial to inframarginal or sometimes even situated within the marginal teeth of the pinnules ; *indusium* delicate, *glandular.* Spores plano-convex, densely covered with prominent irregular, verrucose-saccate projections.

a. **Dryopteris gracillima** var. **gracillima** (Text-fig. 2.)

Fronds small 5–20 cm, lamina elliptic to narrowly ovate, narrowed below, 1·5–4·0 cm broad and four to five times as long, simply pinnate, sub-bipinnate or bipinnate. Sori medial to inframarginal.

CEYLON : *Thwaites C.P. 3383* (BM ; CGE ; E ; K, holotype : PDA, Raxawa, 1855, and Knuckles Mt., Central Province). *Thwaites C.P. 3858* [bipinnate form] (PDA). Hoolankande Peak, Matale, 10 Jan. 1864, ex *Herb. Brodie* (E). On rock face in secondary jungle at Corbet's Gap, 1350 m, 9 Dec. 1950, *Sledge 566* (BM). Same locality, 1440 m, 25 Jan. 1954, *Sledge 1038* (BM). *Wight 1880* (E). *Wall* in *Herb. Beddome* (K). *Wall* (GL).

b. **Dryopteris gracillima** var. **prolongata** Sledge, var. nov. (Text-fig. 3A.)

Frondes 20–50 cm longae, lamina lineari-oblonga 3–6 (8) cm lata usque ad octiens quam longa, omnino simpliciter pinnata vel basi bipinnata. Sori marginales.

CEYLON : Rock crevices in jungle, Gallebodde Rock, Central Province, 27 Jan. 1954, *Sledge 1055* (BM, holotype : K ; US). Midford, Ambagamuwa District, Central Province, 1200 m, 29 Jan. 1954, *Sledge 1066* (BM). *Thwaites* as *C.P. 3062* '*D. deparioides* – state of' (K ; PDA).

c. **Dryopteris gracillima** var. **triangularis** Sledge, var. nov. (Text-fig. 3B.)

Frondes circa 30 cm longae, lamina anguste ad late triangularis, 8–12 cm lata usque ad duplo quam longa, bipinnata. Sori bene intra margines pinnularum.

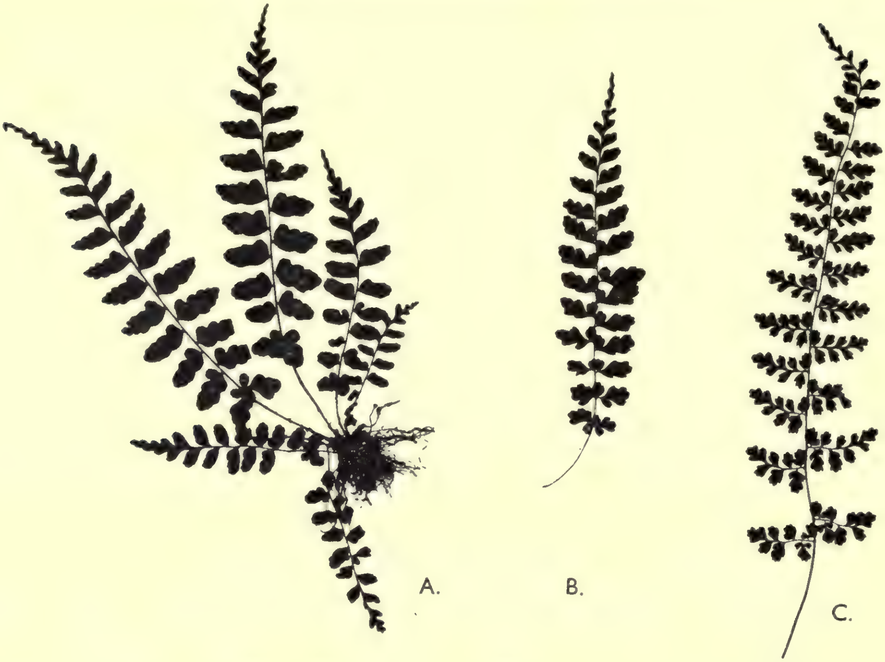

FIG. 2. *Dryopteris gracillima* Ching var. *gracillima*. A: whole plant, pinnate form (*C.P. 3383*). B: frond, sub-bipinnate form (*C.P. 3383*). C: frond, bipinnate form (*C.P. 3858*). All Herb. PDA. × ⅓.

CEYLON: Terrestrial in jungle on Knuckles Mt., Central Province, 1725 m, 30 Jan. 1954, *Sledge 1089* (BM, holotype). *Herb. Brodie* as *C.P. 1368* '*L. sparsa* var. *lata* Moore' (E).

Endemic. (Doubtful from Simla – one plant.)

When Ching named this species he had in mind only those diminutive plants which had originally been distinguished as *Nephrodium sparsum* var. *minus*. But other and larger plants certainly belong to the same polymorphic species. Beddome was aware of this for, in his first reference to it, after alluding to fertile specimens received from Wall with simply pinnate fronds only 2·5 inches high and 0·75 inch broad, he adds 'another form has the fronds 10 inches long and 2 inches broad'. Later, in the Handbook (loc. cit.) he refers to 'larger specimens . . . running into the smaller forms of *deltoidea*'.

When Baker described *Nephrodium sparsum* var. *minus* he adopted Thwaites's manuscript name on a sheet of *C.P. 3383*. Of this there are three sheets at Kew. One of them has three complete plants with fully bipinnate fronds 10–25 × 1·5–4 cm and very small toothed pinnules 3–5 × 2–3 mm. This is the fern described by Baker (loc. cit.). The other two sheets bear different-looking though equally small plants the fronds of which are either simply pinnate with shallowly lobed pinnae or bipinnatifid with few, broad, blunt lobes. One of these sheets has '*Lastrea membranacea* Arn.' added to the label in an unidentified handwriting and Wight's gathering at

Edinburgh is also so labelled, '*Lastrea membranacea* Arnott MSS' being another of the five varieties which Baker listed (loc. cit.) under *Nephrodium sparsum.* But Beddome's statement (*Suppl. Ferns S. Ind. & Brit. Ind.* : 11, 17 (1876)) that *Lastrea membranacea* is the same as *Athyrium macrocarpum* (his interpretation of the latter being based on the allied species *A. anisopterum* – vide Sledge in *Bull. Br. Mus. nat. Hist.* (Bot.) 2 : 289 (1962)) is borne out by a sheet of *A. anisopterum* – *Walker 1880* from Ceylon in herb. Kew – on the label of which is written '*Lastrea membranacea* Arnott in litt. ad Walk.' This is presumably the original *L. membranacea* as validated by Baker (Hook. & Bak., *Synops. Fil.*, ed. 2 : 498 (1874)). Beddome's description of *L. sparsa* var. *minor* was evidently based on the simply pinnate or subbipinnate form, superficially similar to the *Athyrium,* and this is also the form represented on the sheet of *C.P. 3383* in the Peradeniya collection, where plants identical with the

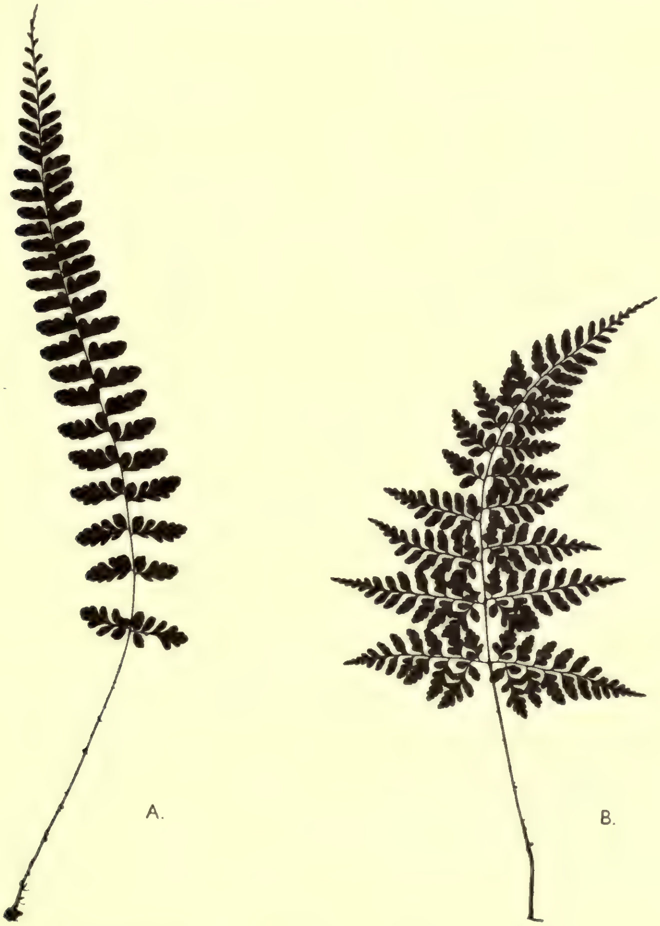

Fig. 3. A : *Dryopteris gracillima* var. *prolongata* Sledge ; frond (*Sledge 1055*).
B : *Dryopteris gracillima* var. *triangularis* Sledge ; frond (*Sledge 1089*). × ⅓.

other dissected and bipinnate form are labelled, evidently in error, *C.P. 3858 Aspidium undulatum*, despite the specimens showing no trace of the zig-zag rhachis and deflexed pinnae which constitute the distinguishing features of that plant. Ching seems to have included both forms in *D. gracillima*. Their markedly different appearance might justify varietal separation though one or two fronds of somewhat intermediate appearance in these and other gatherings might equally well be used as evidence in support of Ching's treatment.

Very small glandular hairs – best observed with a binocular microscope – are present in all the varieties of *D. gracillima*. The only other glandular species of *Dryopteris* in Ceylon is *D. ambigua*. The hairs are unicellular with a globular and glandular head. They are plentiful on the stipe, rhachises and surfaces of the pinnae and are also found on the indusia and rhizome scales. In time many of these glands are shed or abraded and in old herbarium specimens a careful search may be necessary to verify their presence. They persist especially on the proximal parts of the abaxial surfaces of the pinnae and about their points of attachment to the rhachis. On young rhizome scales a few glands are usually present on the margins and some sessile glands on the surfaces, but on older scales they may no longer be evident. They are usually conspicuous, under appropriate magnification, both on the edges and on the dorsal surfaces of the indusia.

The small size of var. *gracillima* alone distinguishes it from all other Ceylon species of *Dryopteris*. Fronds not exceeding 5 cm in length including the stipe may be fertile. But it is by no means certain that all such small fertile plants belong to the same species. Some very small plants with simply pinnate, narrowly elliptic fronds identical in cutting and not exceeding 12 cm in length have their sori situated near the ends of the pinnule teeth as in *D. deparioides*, to which species such plants were referred by Thwaites. It is possible that these are indeed juvenile specimens of *D. deparioides* which are precociously fertile, for it is very likely that young fronds in that species are markedly different in form from fully mature ones. But we do not know what yearling plants of *D. deparioides* are like. Other plants identical in size and outline have their sori well within the margins of the pinnules. Such plants are labelled var. *minor* or *D. gracillima*, but I see no difference save in the position of the sori. Both are glandular. Soral position in *D. gracillima* is certainly subject to considerable variation since in var. *prolongata* the sori may lie within the marginal teeth of the pinnules as in *D. deparioides*.

The var. *prolongata* is notable for its long, slender, very narrow fronds, commonly only 2–4 cm in width and up to eight times as long. It normally has considerably longer stipes than in var. *gracillima*. The sori may lie close to the margins of the pinna lobes or they may even migrate into the marginal teeth. Such plants were regarded by Thwaites as a state of *D. deparioides* and one of his gatherings in the Peradeniya Herbarium is remarkable not only in the sori being situated very near the extremities of the teeth, but many are also situated at the summits of conspicuously raised columns of tissue as in *Peranema cyatheoides*. Other sori on the same fronds are sessile.

The status of var. *prolongata* is uncertain and can only be determined by observations on living plants. My Gallebodde plants (*Sledge 1055*) look so very different from var. *gracillima* that their relationship could well pass unsuspected. But they came from a shady locality and, although none of the eight complete plants bear fronds which show any transition to var. *gracillima*, they may represent an extreme state induced by shady conditions.

The var. *triangularis* is distinguished by its considerably broader more deltoid fronds which are widest at the base. It was doubtless to such plants that Beddome referred when he alluded (*Handb. Ferns Brit. Ind.* : 254 *sub L. sparsa* var. *minor* (1883)) to 'larger specimens . . . running into the smaller forms of *deltoidea*', though the similarity extends only to frond outline. It is much closer to *D. ambigua* which has the same minutely gland-studded fronds, but it differs in its non-caudate pinnae, in its broadened more triangular lower pinnae, its pinnules being less unequal at the base, and in its sori not being situated close to the margins of the pinnules. Its spores are also identical with those of *D. gracillima*. Some young specimens of mine show fronds intermediate in form between var. *triangularis* and var. *prolongata* and it may be another growth form ; but typically it is so distinct in appearance that, like var. *prolongata*, its connexion with *D. gracillima* is far from obvious.

As regards the relationship of *D. gracillima*, I do not think it is at all closely allied to *D. sparsa* though often the lobes of the pinnae or the pinnule segments have a small sharp tooth on the anterior border as in *D. sparsa*. Ching (loc. cit.) considered it closely related to Moore's *Lastrea gracilis*, which he transferred to *Dryopteris*. I see no resemblance whatever, other than size. It is indeed very doubtful if Moore's species is a *Dryopteris* ; the polystichoid teeth and eccentrically peltate indusia lend more support to Clarke's view (in *Trans. Linn. Soc. Lond.*, Ser. 2, Bot. 1 : 508 (1880)) that it is a *Polystichum* – a view which Ching refuted without advancing any evidence for doing so.

Clarke's statement (in *Trans. Linn. Soc. Lond.*, Ser. 2, Bot. 1 : 524 (1880)) that Edgeworth's Simla example 'agrees exactly with Thwaites'' is true in so far as it refers to a single whole plant mounted on the same sheet as the fronds of *Athyrium anisopterum* (*Walker 1880*) referred to above. Other examples of Edgeworth's from N. India and Godwin Austen's North Cachar frond (mounted on the same sheet as the Simla plant) are all *A. anisopterum*. I have seen no other specimens from the Himalayas or elsewhere which match Ceylon plants of *D. gracillima*.

9. ***Dryopteris ambigua*** Sledge, sp. nov. (Text-fig. 4.)

Lastrea sparsa var. *purpurascens* Trimen in J. Ceylon Brch R. Asiat. Soc. 9 : 115 (1885) pro parte, non *Aspidium purpurascens* Blume.

Rhizoma erectum, paleis lanceolatis, brunneis, acutis, circa 5 mm longis vestitum. Frondes 20–40 (60) cm longae ; stipites 10–20 cm, paleis patulis atque glandulis minutis, rhachides similiter glandulosae atque squamosae saltem prope axillae pinnarum. Lamina bipinnata praeter versus apicem tam longa quam stipes vel longior, in ambitu anguste ad late triangulari-ovata, 10–20 cm lata, interdum minus, plerumque sesqui vel duplo longior ; *pinnae* anguste oblongae, patentes vel ascendentes, 5–15 cm longae, *plerumque caudatae, infimae aequales vel parum abbreviatae, pinnulis basiscopicis non vel paulo majoribus quam acroscopicis, rhachides glandulosae* ;

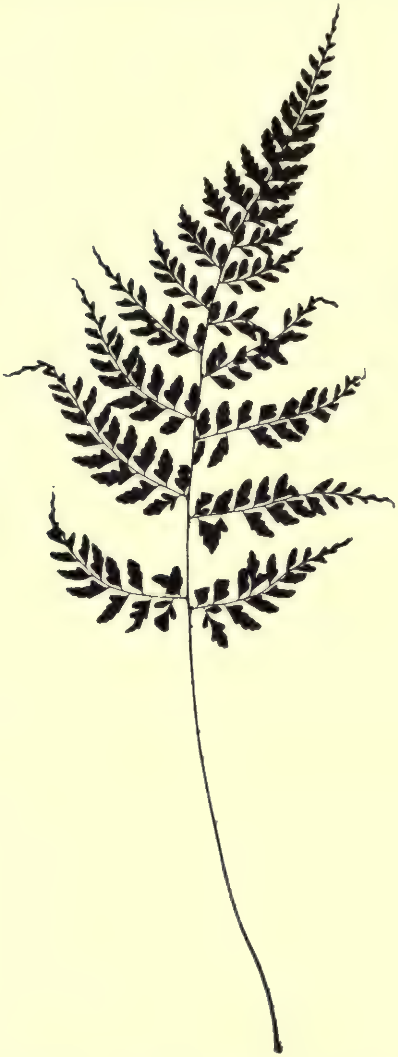

FIG. 4. *Dryopteris ambigua* Sledge. Frond (*Sledge 1164*). × ⅓.

pinnulae petiolatae anadromicae, basi inaequales, ovatae, basibus superioribus plus minusve auriculatis, basibus posticis anguste cuneatis, apices obtusae, margines subintegrae vel leviter lobatae, infra pinnatifidae, infimae aliquando penitus pinnatae, glabratae praeter glandulas minutas illis in pinna rhache similia ; textura chartacea. Sori prope marginem pinnularum ; *indusium glandulosum*, tenue, non perdurans. Sporae plano-convexae paginae mamillatis verrucoso-saccatis dense obtectae.

CEYLON : *Thwaites C.P. 1370* (BM ; CGE ; E ; K, holotype ; PDA, Dimboola June 1848 *Gardner*, and Kotmalie, March 1869). Tonacombe, Uva Province, 1320 m,

21 Feb. 1954 *Sledge 1164* (BM; K; US). Same locality, *Freeman 253B, 254C, 255D* (BM). 1899, *Herb. Anderson* (one frond) (E).

Endemic.

Specimens of *Thwaites C.P. 1370* distributed as *Nephrodium sparsum* are represented in many herbaria and are all clearly conspecific. They differ from *D. sparsa* in their glandulosity, their smaller pinnules, often caudate pinnae and in the basiscopic pinnules of the lowermost pinnae being little if at all enlarged. Their distinctness had been recognized by others, for Trimen (*J. Ceylon Brch R. Asiat. Soc.* 9 : 115 (1885)) separated *C.P. 1370* as *L. sparsa* var. *purpurascens* and two of the Kew sheets have been annotated *L. caudata* Moore, a name which Moore however never published.

Though there is no obvious similarity between typical examples of *D. ambigua* and *D. gracillima* I have no doubt that the former is more closely related to the latter than to any other Ceylon species. Large fronds of *D. ambigua* look more like *D. deparioides* subsp. *concinna* save in their smaller size, more triangular outline, their glandular fronds, and the presence of scales on the rhachis. Some small plants approach *D. gracillima* var. *triangularis* closely. The differences are referred to under that species. My Tonacomb plants have spores which are considerably larger than those of *D. gracillima.*

The relationship between *D. ambigua, D. gracillima* and the varieties of the latter needs investigation. My collections of all of these contain good spores and there is no reason to suspect that hybrid swarms are involved.

10. **Dryopteris deparioides** (T. Moore) Kuntze, Rev. Gen. Pl. 2 : 812 (1891).

Diclisodon deparioides T. Moore, Index Fil. : xcvi (Apr. 1857) ; 316 (1861).
Aspidium deparioides (T. Moore) Hook., Fil. Exot. : t. 3 (Sept. 1857).
Nephrodium deparioides (T. Moore) Hook., op. cit. : t. 60 in obs. (1858) ; Sp. Fil. 4 : 139 (1862).
Lastrea deparioides (T. Moore) Bedd., Ferns S. Ind. : 36, t. 104 (1863) ; Handb. Ferns Brit. Ind. : 257 (1883).
Aspidium concinnum Thwaites, Enum. Pl. Zeyl. : 392, 438 (1864 sero) non *Aspidium concinnum* Link (1833).
Lastrea concinna Bedd., Ferns S. Ind. : 82, t. 247 (Sept. 1864) non *Lastrea concinna* (Willd.) T. Moore (1858).
Nephrodium thwaitesii Bak. in Hook. & Bak., Synops. Fil. : 277 (1867).
Lastrea thwaitesii (Bak.) Bedd., Suppl. Ferns S. Ind. & Brit. Ind. : 18 (1876) ; Handb. Ferns Brit. Ind. : 258 (1883).
Dryopteris thwaitesii (Bak.) Kuntze, Rev. Gen. Pl. 2 : 813 (1891).
Dryopteris emigrans Copel. in Univ. Calif. Publs Bot. 12 : 392 (1931), *nom. superfl.*

Rhizome erect, its apex and the lower parts of the tufted stipes clothed with narrow, acute, entire, pale brown scales. Fronds up to 75 cm long, 25 cm broad. Stipes up to 30 cm scaly below, naked above ; rhachis smooth, bearing numerous very short, unicellular, club-like or globular, papillate hairs in the dorsal groove about the junction with the pinna rhachides which are similarly papillate above. Lamina bipinnate, ovate to oblong-ovate in outline with shortly stalked pinnae, the basal pair or pairs slightly reduced, glabrous on both surfaces ; pinnules anadromic 1–2 (3) cm long, not contiguous, rhomboid-ovate or oblong, dentate, lobed or laciniato-pinnatifid, posterior base cuneate and decurrent, anterior base truncate or rounded, often subauriculate, *basiscopic pinnules of lower pinnae not enlarged. Sori* (in subsp. *deparioides*) *nearly terminal on the prominent marginal teeth of the pinnules, or* (in subsp. *concinna*) situated *just within the pinnule margin.* Spores monlete, 42–45 × 25–27 μm with a perispore forming an undulate wing and convoluted surface folds.

a. subsp. ***deparioides***

Sori nearly terminal on the prominent, narrow, marginal teeth of the pinnules and larger than the teeth which bear them.

CEYLON : *Thwaites C.P. 3062* (BM ; K ; PDA ; one of the PDA sheets localized Hantane, Jan. 1854, one of the K. sheets localized Ambagamuwa, 1863). Kottawa forest near Galle, *Ferguson* (PDA). Adam's Peak, Ratnapura side at 300–450 m, in forest, 5 Jan. 1951, coll. *I. Manton, Sledge 826* (BM ; K). *Wall* (K). *Robinson* (K). *Skinner* (K). *Trimen* in *Herb. Beddome* (K). *Hance 112* ex *Bradford* (BM). Hort. Kew ex *Herb. J. Smith* (BM).

b. subsp. ***concinna*** C. Chr., Index Fil., Suppl. 3 : 84 (1934).

Aspidium concinnum Thwaites, loc. cit., non *A. concinnum* Link.
Lastrea concinna Bedd., loc. cit., non *L. concinna* (Willd.) T. Moore.

Sori intramarginal situated at the base of the short, broad, marginal teeth of the pinnules.

CEYLON : *Thwaites C.P. 3798* (BM ; CGE ; K, holotype ; PDA ; one sheet at K and one at PDA localized : Sinha Raja forest, April 1863). Sinha Raja forest above Beverley Estate, Deniyaya, 900 m, 12 March 1954, *Sledge 1273* (BM ; K). *Wall* (K). *Beddome* (K). *Skinner* (K). *Hance 11303* ex *Thwaites* (BM).

South India : Anamallay Hills (subsp. *deparioides* only).

One of the most remarkable and distinct of all species of *Dryopteris* on account of the position of the sori at or near the extremities of the slender pinnule teeth, where they are very conscpicuous due to their size exceeding that of the outgrowths on which they are borne.

The fern which Thwaites (op. cit. : 392) described as *Aspidium concinnum* is superficially so distinct that originally he compared it with *Aspidium sparsum* D. Don, but later in the same work (op. cit. : 438) he states : 'Frondes steriles vix ab iis *A. deparioidis*, Hook., distinguendae, cui haec planta valde affinis et forsan ejusdem solum varietas.' Beddome maintained it as a species in the *Handbook* though with some doubt ; the only distinctions from *D. deparioides* which he cites being that 'the pinnules are less cut and the segments bluntly lobed instead of having prominent teeth, and the sori just within the margin'. In *D. deparioides* however the pinnules are variable in form: they may be subpinnatifid or they may be quite devoid of lobes and furnished only with the prominent marginal teeth at the extremities of which the sori are borne. The pinnules of such forms are considerably less cut than those of some forms of subsp. *concinna*. I find no differences in scales, spores or other characters. Hence only the position of the sorus remains as a valid difference between the two taxa.

Beddome suggested that *concinna* was probably the normal form of *D. deparioides* and certainly the latter must be the derivative condition. In *D. gracillima* there is a similar variation in position of the sori, which may occupy every intermediate position from intramarginal to subterminal. Indeed in some forms the sori may not only be situated quite as far out on the teeth as in *D. deparioides* but may even be raised on a stout column of tissue as in *Peranema cyatheoides*. *D. deparioides* and subsp. *concinna* on the other hand appear to be quite distinct as regards their soral positions and not to be connected by any intergrading forms. The former is the more widely distributed of the two occurring in the central and southern provinces of Ceylon and in the Anamallay Hills in southern India, where, however, it appears to be very rare, Beddome's original gathering from there being the only one at Kew. The subsp. *concinna* has only been recorded from the Sinha Raja Forest in southern Ceylon. There are therefore geographical grounds in support of Christensen's treatment of this as a subspecies.

Copeland (loc. cit.) was in error in suggesting that the basionym of *Dryopteris thwaitesii* Kuntze is *Meniscium thwaitesii* Hook.; it is based on *Nephrodium thwaitesii* Baker, a nomen novum for the later homonyms *Aspidium concinnum* Thwaites and *Lastrea concinna* Bedd. whose relative dates of publication are uncertain.

3. *POLYSTICHUM* Roth

POLYSTICHUM Roth, Tent. Fl. Germ. 3: 69 (1799).

Rhizome erect, scales fimbriate or lacerate and often polymorphic; fronds simply pinnate, bipinnate or tripinnate, rarely more divided, anadromic, nearly always narrow in outline or if broad never dilated at the base and never with the basal pinnae basiscopically enlarged, sometimes bearing gemmiferous buds, stiff to hard in texture with the pinnules or their segments usually spinulose-serrate; indusium peltate, sometimes absent or vestigial.

Ceylon representatives of *Polystichum* display most of the characters typical of the genus and are readily separable from *Arachniodes* and *Dryopteris*. In *P. setiferum* var. *nigropaleaceum* however the texture of the frond is soft and no less than four of the species are exceptional in that the sori are either exindusiate or the indusium is vestigial or rudimentary. The fronds are simply pinnate in *P. auriculatum* and bipinnate in other species save in *P. anomalum* where they are sometimes tripinnate. In the polymorphic *P. walkerae* the fronds may be simply pinnate, bipinnate or tripinnate. This species has previously been included both in *Dryopteris* and *Arachniodes* but clearly belongs here. The variable nature of the scales clothing the rhizomes and stipes is well shown in *P. anomalum*, *P. biaristatum*, *P. tacticopterum* and *P. setiferum* var. *nigropaleaceum*, in which are found a mixture of broad (concolorous or bicolorous), narrow and filiform scales.

KEY TO SPECIES OF *POLYSTICHUM*

Fronds pinnate :
  Pinnae prominently auriculate, bases very unequal . . 1. *P. auriculatum*
  Pinnae not auriculate, bases equal or subequal . . . 2. *P. walkerae*
Fronds bipinnate, or rarely tripinnate :
  Scales of stipe all concolorous, brown ; sori exindusiate or indusium rudimentary :
    Axes with filiform, entire or sparsely toothed scales . . 2. *P. walkerae*
    Axes with mixed filiform and broad scales, the latter with pale, copiously fringed margins . . . . 3. *P. anomalum*
  Scales of stipe not all concolorous, some with black centres :
    Sori normally exindusiate (invariably so in Ceylon) . 4. *P. tacticopterum*
    Sori indusiate :
      Fronds stiff, pinnules subsessile, margins serrate above 5. *P. biaristatum*
      Fronds soft, pinnules stalked, margins with setiform or aristate teeth 6. *P. setiferum* var. *nigropaleaceum*

1. ***Polystichum auriculatum*** (L.) C. Presl, Tent. Pterid. : 83 (1836).—Bedd., Ferns S. Ind. : 41, t. 120 (1864) ; Handb. Ferns Brit. Ind. : 203, fig. 102 (1883), excl. vars.

Polypodium auriculatum L., Sp. Pl. 2 : 1088 (1753).

Rhizome erect, scaly ; fronds tufted, up to 80 cm long. Stipe nearly as long as the lamina, scaly, the scales lanceolate, attenuate, thin, pale brown with peltate bases and irregularly fimbriate margins ; rhachis similarly scaly. *Lamina* 30–60 × 5–10 cm, oblong, *pinnate* with 20–30 or more pairs of horizontal, sessile or subsessile pinnae ; *pinnae* oblong or broadly lanceolate, falcate, base very unequal, *broadly truncate above with a prominent, sharply pointed auricle*, excised below, margins serrate, apex acute, lower surface with scattered, pale, fimbriate scales on the veins when young, upper surface glabrous ; texture chartaceous. Sori in two rows (save in the auricle), one on each side of the midrib ; indusium fugacious, often quite absent.

CEYLON : *Thwaites C.P. 1366* (BM ; E ; K ; PDA, Peacock Mt. and Ramboda, 1847, *Gardner*). *Gardner 1095* (CGE, Hantane, Aug. 1844, forests on Adam's Peak, March 1846 ; K). Kandy, *Mrs Chevalier* (BM). Nuwara Eliya, *Freeman 208A*, *210C* (BM). Blackpool, *Freeman 209B* (BM). Hantane, 1140 m, 8 Dec. 1950, *Ballard 1046* (K). Hakgala, 1800 m, 16 Dec. 1950, *Sledge 634* (BM). Same locality, 23 Dec. 1950, *Sledge 705* (BM). Between Hakgala and Nuwara Eliya, 1650 m, 23 Dec. 1950, *Sledge 708* (BM). Nawanagala, near Madugoda, 1110 m, 8 Jan. 1954, *Sledge 944* (BM). *Walker* (K). *Robinson 132* (K). *Wall* (E ; PDA). *Naylor Beckett 42* (E).

Common in forests of the Central Province above 1000 m.

South India.

2. ***Polystichum walkerae*** (Hook.) Sledge, comb. nov.

Polypodium walkerae Hook., Sp. Fil. 4 : 233 (1862).—Bedd., Ferns S. Ind. : 78, t. 234–5 (1864).

Polypodium elongatum sensu Thwaites, Enum. Pl. Zeyl. : 394 (1864), excl. forma *c* ; non Aiton nec Wall. ex Hook.

Nephrodium walkerae (Hook.) Bak. in Hook. & Bak., Synops. Fil., ed. 2 : 493 (1874).

Lastrea walkerae (Hook.) Bedd., Suppl. Ferns S. Ind. & Brit. Ind. : 16 (1876) ; Handb. Ferns Brit. Ind. : 233 (1883).

Dryopteris walkerae (Hook.) Kuntze, Rev. Gen. Pl. 2 : 814 (1891).—C. Chr., Index Fil. : 301 (1906).

Rumohra walkerae (Hook.) Ching in Bull. Fan meml Inst. Biol., Bot. 8 : 496 (1938).

Arachniodes walkerae (Hook.) Ching in Acta bot. sin. 10 : 260 (1962).

Rhizome erect, clothed at the apex and about the bases of the tufted stipes with lanceolate, acuminate, brown scales up to 15 × 5 mm with toothed margins. Fronds up to 1 m long or more ; stipe and rhachis scaly with linear, dark brown *scales with fimbriate bases and sparsely toothed margins*. *Lamina* narrowly lanceolate to oblong-ovate in outline, *very variable in cutting*, either *simply pinnate* with shortly stalked, lanceolate, acuminate, subentire pinnae with subequal, rounded or cuneate bases, 5–15 × 1–2 cm, *or pinnae dentate, crenate-lobate, deeply lobed, or pinnatipartite* to the narrowly winged pinna rhachis, *or pinnately divided* into about 25 pairs of pinnules the basal ones at least quite free and stalked, up to 20 × 5 cm in bipinnate forms with the pinnules unequally oblong-ovate, the posterior margin straight or narrowly cuneate, anterior margin broadly cuneate to truncate, obscurely auriculate, usually with a few more or less sharp serrations towards the blunt apex, the margins otherwise subentire or somewhat repand or more or less lobed ; under surfaces deciduously fibrillose on the veins, upper surfaces glabrous ; texture subcoriaceous. Sori terminal on the veins usually forming two, rarely three, rows on each side of the costa, or a single row on each side of the midrib of the pinnule in bipinnate forms ; *indusium normally absent*, if present vestigial and centrally situated amongst the sporangia. Spores monolete with a winged perispore.

a. var. ***walkerae***

Fronds simply pinnate with subentire, dentate, lobed or pinnatifid pinnae, or the pinnae fully pinnate.

CEYLON : Adam's Peak, *Walker* (K, holotype). Same locality, March 1846, *Gardner 1256* (CGE ; K). Same locality, *Moon* (BM). Same locality, leg. *I. Manton*, 5 Jan. 1951 [simply pinnate], *Sledge 827* (BM). Same locality, 690 m, 9 March 1954 [simply pinnate], *Sledge 1244* (BM). *Thwaites C.P. 3276* (BM ; K ; PDA, localities indicated on PDA sheets : Saffragam, May 1821, *Moon* ; Ambagamuwa, Dec. 1854, 1862; Adam's Peak). *Thwaites C.P. 3286* (BM; K). Ambagamuwa district, *Hance 16836* ex *Thwaites C.P. 3276* (BM). Panilkanda, near Deniyaya, 600 m, 24 Jan. 1951 [simply pinnate and bipinnate], *Sledge 923, 923A, 923B* (BM). Same locality and date, *Ballard 1560* (K). Gallebodde, by stream in jungle, 600 m, 26 Jan. 1954 [simply pinnate], *Sledge 1041* (BM). Sinha Raja forest above Beverley estate, Deniyaya, 900 m, 12 March 1954 [bipinnate], *Sledge 1271* (BM). Kotmalee, 1847, *Fortescue* (CGE). 'Type of tab. 234', ex *Herb. Beddome* (K). 'Type of tab. 235 var. *macrocarpa* and var. *pinnatifida*' ex *Herb. Beddome* (K). *Robinson 187* (K). *Wall* (K). Ex *Herb. Hooker*, 1853, in *Herb. J. Smith* (BM). 1866, *Herb. J. Smith* (BM).

b. var. ***bipinnatum*** (Bedd.) Sledge, comb. nov.

Polypodium walkerae var. *bipinnatum* Bedd., Ferns S. Ind.: 78, t. 235 fig. inf. (1864).
Lastrea walkerae var. *bipinnata* (Bedd.) Bedd., Handb. Ferns Brit. Ind.: 234 (1883).
Rumohra walkerae var. *bipinnata* (Bedd.) Ching in Bull. Fan meml Inst. Biol., Bot. 8: 497 (1938).

Fronds larger than in var. *walkerae*, bipinnate with the pinnules becoming progressively more deeply lobed from above downwards, those of the lowermost pinnae up to 9 cm long and pinnatipartite or quite pinnate.

CEYLON: 'Type of tab. 235 *L. walkerae* var. *bipinnata*', ex *Herb. Beddome* (K, holotype). Ambagamuwa, in jungle, 570 m, 19 Jan. 1954, *Sledge 995* (BM). Laxapana, 900 m, 28 Jan. 1954, *Sledge 1059* (BM). *Trimen* ex Ceylon Herb. (K). *Thwaites C.P. 3286e* (PDA).

Forests of the Central, Southern and Sabaragamuwa Provinces, up to 900 m.

Endemic.

Hooker based his description of this species on plants collected on Adam's Peak. The type is described as having simply pinnate fronds the lower pinnae of which are 'more or less (but never deeply) lobato-pinnatifid'. Subsequent gatherings from other localities included plants with fronds ranging from simply pinnate with subentire pinnae to subtripinnate forms and all fully fertile. A parallel range of variation is shown in *Arachniodes assamica* (Kuhn) Ching, in which plants with compound leaves are treated as the typical condition and those with simple leaves as reduced forms. The series should perhaps be read in the same way in *P. walkerae*. On a sheet in Herb. Kew there is a note by Wall: 'I have a strong impression that the simple forms eventually become more compound as the roots become older.' At Deniyaya I collected fronds with almost entire pinnae (*Sledge 923*), with deeply lobed pinnae (*Sledge 923A*), and with pinnatipartite to completely pinnate pinnae (*Sledge 923B*), corresponding to the varieties *walkerae*, *macrocarpa* Bedd. and *pinnatifida* Bedd., all from the same population. Furthermore, a plant with dentate pinnae collected on Adam's Peak in 1950, which still remains in cultivation at Leeds, has since produced fronds in which the pinnae are fully pinnate. It is clear therefore that the 'varieties' *macrocarpa* and *pinnatifida* are no more than growth forms, the state of division of the fronds being merely an expression of age or environmental factors. The phenomenon of precocious fertility in fronds of morphologically immature form is not uncommon amongst Ceylon ferns and I have drawn attention to it elsewhere (*Bull. Br. Mus. nat. Hist.*, Bot. 2 : 278 (1962)). In *P. walkerae*, as in the instance of *Diplazium dilatatum* cited in my paper, factors other than age alone are almost certainly concerned in the change from a simply pinnate to a more divided state of the frond, for robust fronds from Adam's Peak more than three times the length of the bipinnate fronds produced in cultivation were simply pinnate, as are all other gatherings which I have seen from there. Herbarium specimens also show no relationship between size of frond and state of division.

There remains however another robust plant with broader fronds, the lower pinnae of which are bipinnate (i.e. the frond is tripinnate) and up to 30 cm long with pinnules up to 9 cm long. This has been included under *P. walkerae* as var. *bipinnatum*. It is evidently a much rarer fern judging from the few examples represented in herbaria. Thwaites expressed the view (*Enum. Pl. Zeyl.* : 394, 1864) that it was probably a distinct species. I find no difference in the colouration of dried specimens, to which he referred, but I do not exclude Thwaites' view although I am unable to see any significant difference other than its greater size and degree of division. The upper part of the frond in such specimens is no different from the lower part in 'var. *pinnatifidum*'. Yet it seems improbable that my two gatherings of this would not have been accompanied by simply pinnate or bipinnate fronds if they were growth forms. This plant requires further study in the field, pending which it is best retained as a variety under *P. walkerae*.

Baker (loc. cit.) was the first to detect an indusium in this species, and he transferred it from *Polypodium* to *Nephrodium*, remarking of it 'inv. very fugacious'. Two years later Beddome transferred it to *Lastrea* without any statement as to the form of the indusium. Later, in his *Handbook*, he attributed a 'reniform' indusium to it. Nearly all specimens of *P. walkerae* are in fact exindusiate and where indusia are present – and in all my specimens I can detect them only in my two gatherings of var. *bipinnatum* and not in all sori of these – they are vestigial and rudimentary and are dryopteroid only in the sense that they are open on one side. As it is only to be expected that a vestigial or reduced indusium if derived from an eccentrically peltate one would be open on one side, the form of such a partially abortive indusium cannot be properly classified as either polystichoid or dryopteroid and is of no significance in determining generic relationships. Moreover, although in *P. biaristatum* and *P. auriculatum* (and doubtless in other species) the indusia are peltate and centrally attached, eccentric indusia are commonly developed and a search will often reveal some indusia which are open on one side. More significant than the indusial sinus is the fact that the indusium when formed arises from the centre of the sorus and is surrounded on all sides by sporangia.

In its erect habit, the generally narrow outline of its fronds and in its subcoriaceous texture *P. walkerae* is a typical *Polystichum*, differing only in the absence of spinulose teeth on the margins of the pinnae or pinnules. When Ching transferred this species to *Rumohra* he stated that it differed from *Polystichum* 'in the creeping rhizome, distant leaves and the Dryopteroid type of indusium'. All three of these statements are false : the rhizome is erect, the fronds are clustered and the indusium is not dryopteroid! Later Ching transferred it to *Arachniodes* although the frond outline of the simply pinnate type is elliptical with the lowermost pinnae slightly reduced. In the more divided varieties the arrangement of the pinnules is anadromic but only in var. *bipinnatum* do the fronds become more deltoid in shape with a weak basiscopic enlargement of the basal pinnae, which are not however markedly deltoid in outline as in species of *Arachniodes*. Whilst there would be more justification in placing such plants in *Arachniodes* than ever there was in transferring *P. walkerae* to that genus, it would be ill advised in my opinion to separate them specifically – and still more so generically – without further information derived from the living plant.

3. ***Polystichum anomalum*** (Hook. & Arn.) J. Smith, Ferns Brit. & For.: 151 (1866).—Bedd., Ferns Brit. Ind.: t. 219 (1867).

Polypodium anomalum Hook. & Arn. in Hooker's J. Bot. 8 : 360, t. 11 (1856).
Aspidium anomalum (Hook. & Arn.) Hook., Sp. Fil. 4 : 27 (1862).
Aspidium biaristatum sensu Thwaites, Enum. Pl. Zeyl. : 390 (1864) ; non Blume.
Phegopteris eximia Mett. apud Kuhn in Linnaea 36 : 107 (1869).
Polystichum biaristatum sensu Wu, Wong & Pong in Bull. Dept. Biol. Coll. Sci. Sun Yatsen Univ. 3 : 84, t. 33 (1932) ; non T. Moore.
Polystichum squarrosum sensu Wu, Wong & Pong, tom. cit. : 86, t. 34 (1932) ; non Fée.
Polystichum eximium (Mett.) C. Chr. in Bull. Dept. Biol. Coll. Sci. Sun Yatsen Univ. 6 : 8 (1933) ; Index Fil., Suppl. 3 : 163 (1934).

Rhizome erect, scaly ; fronds tufted, up to 2 m long. Stipe about equalling the lamina, very scaly, *scales lanceolate to broadly oval*, up to 20 × 10 mm, with attenuate pointed apices and *pale, strongly fringed margins, mixed with smaller, narrower ones and appressed scurfy scales with long-fimbriate margins* and *all* thin, brown and *concolourous. Lamina* up to 1 m, ovate-lanceolate, *bipinnate or tripinnate below* in large fronds, texture stiffly chartaceous ; *main rhachis paleaceous* with abundant, very slender, tapering *scales with long-fimbriate margins and some broader*, lanceolate to ovate, acute, light brown to rufous brown *scales with pale, ciliate-fringed margins* ; pinna rhachides similarly clothed with pale brown, thin scales ; pinnae shortly stalked, alternate, or sub-opposite below, well spaced, oblong or lanceolate-oblong, acuminate, patent and often falcate, up to 25 × 10 mm, but often smaller, basal pair not reduced ; *pinnules* 15–30 (70) mm, *unequally ovate*, lower ones shortly stalked, becoming sessile then adnate distally, posterior base excised or cuneate, *anterior base truncate and auriculate*, apex acute or apiculate, margins subentire, serrate, dentate, lobed, pinnatifid or quite pinnate below in large fronds, basal acroscopic pinnules often enlarged and more deeply lobed, under surfaces with pale, hair-like fibrils on the veins, upper surfaces glabrescent. Sori forming a line on either side of the midrib of each pinnule and of its basal lobe, mostly near to the costa ; *indusium absent* or rarely a vestigial indusium present.

a. var. ***anomalum***

Polystichum aculeatum var. *anomalum* (Hook. & Arn.) Bedd., Handb. Ferns Brit. Ind. : 209 (1883).—C. Chr., Index Fil. : 577 (1906).

Sori on upper surface of pinnules.

CEYLON: *Mrs Walker* (K, holotype). *Thwaites C.P. 3504* (BM; K; PDA, Haputale and below Horton Plains, 1500–2100 m, April & May 1856, Feb. 1857). Namunakula, 29 April 1907, *J. C. Willis* (PDA). Same locality, *Freeman 217A, 218B* (BM). Same locality, 1680 m, 24 Feb. 1954, *Sledge 1198* (BM). Ohiya Valley below Horton Plains, Sept. 1890, no collector's name (PDA). Path to Haldumulla from Horton Plains, abundant, Sept. 1890, no collector's name (PDA). Upper part of Kalupahane valley, 23 Feb. 1882, no collector's name (PDA). Above Nonpareil Estate, abundant, 24 Feb. 1882, no collector's name (PDA). 'Type of tab. 219', ex *Thwaites* in *Herb. Beddome* (K).

b. var. ***travancoricum*** (Bedd.) Sledge, comb. nov.

Polystichum aculeatum var. *travancoricum* Bedd., Handb. Ferns Brit. Ind.: 209 (1883).

Sori ventral.

CEYLON: *Thwaites C.P. 3275* (BM; K; PDA, between Nuwara Eliya and Maturata, 2100 m, Feb. 1857). Nuwara Eliya, *Freeman 213D* (BM). Frotoft Jungle, *Freeman 215F* (BM). In jungle by side of track from Pattipola to Horton Plains, 2025 m, 20 Dec. 1950, *Sledge 710* (BM). Le Vallon Estate, 1230 m, 9 Feb. 1954, *Sledge 1101* (BM). *Freeman 218C* (BM). *Gardner 1102* (K). *Mrs Walker* (K). *Wall* in *Herb. Beddome* (K).

Forests of the Central and Uva Provinces, 1200–2100 m.

South India, Tonkin, Thailand, S. China (Kwangsi). The var. *anomalum* endemic.

This is a case where an anomalous form was described as a new species on the basis of its peculiar characteristic before the normal form of the species had been distinguished.

Mettenius based his description of *Phegopteris eximia* on Ceylon specimens of Thwaites *C.P. 3275*. Plants from the Nilgiri district of South India (e.g. *Gamble 13397, 20591* in Herb. Kew) are certainly the same species and the type of Beddome's *Polystichum aculeatum* var. *travancoricum* from Tinnevelly Ghats (Herb. Kew) is also a large tripinnate and indusiate form of the same species. It has the copiously fringed and pale margins to the scales which are very distinctive in this species.

The type of *Phegopteris eximia* was described as exindusiate, which is usually the case in this species; but Christensen (loc. cit.) could find no difference other than the presence of an indusium in plants from Tonkin and South China and concluded that indusia were probably normally present but very fugacious. I have been able to verify the presence of vestigial indusia on some young fronds of my Ceylon gatherings of both varieties of *P. anomalum*, but usually the indusium is wholly lacking even in young sori. Ching's *P. fibrillosum* from Kwangtung, which Christensen equated with *P. eximium*, is certainly not the same species, and Tagawa's inclusion (in *Acta phytotax. geobot. Kyoto* 10: 282 (1941)) of Formosa in the distribution of *P. eximium* was based on the identity of specimens from there with Ching's species.

The var. *anomalum*, which is remarkable in producing its sori on the upper surfaces of the fronds, is unknown outside Ceylon. In other respects it differs in no way from *P. eximium*, to which its relationship was already recognized by Mettenius.

Occasionally some sori are produced on the under surfaces of the pinnules and I have one frond in which both dorsal and ventral sori are present on the same pinnules. Older writers no doubt included both varieties in *P. anomalum*, for Hooker and Baker (*Synops. Fil.* : 254 (1867)) state that the sori are 'often upon the upper surface' and Beddome (*Handb. Ferns Brit. Ind.* : 209 (1883)) says 'sori often, but not always, on the upper surface'. There are also two sheets of Wall's in Herb. Kew (ex Herb. Beddome) with fronds showing wholly ventral sori yet queried by Beddome as *P. aculeatum* var. *anomalum*.

P. anomalum differs from *P. biaristatum* in its larger fronds and concolorous scales, the largest of which are double the width of those of *P. biaristatum* with margins which, when not abraded, are pale coloured and closely ciliate-fringed rather than fimbriate. The rhachis is more densely clothed with narrow, strongly fimbriate scales and the pinnules are acute or sharply acute at the apex but their margins are not spinulose-serrate, their lobes being bluntly rounded. The sori are normally exindusiate, or less commonly with a vestigial and evanescent indusium, and they are situated nearer to the midrib than to the margins of the pinnules. In *P. biaristatum* the sori are conspicuously indusiate and frequently situated nearer the margin than the midrib. The two species also differ cytologically, *P. biaristatum* being tetraploid and *P. anomalum* hexaploid.

4. ***Polystichum tacticopterum*** (Kunze) T. Moore, Index Fil. : 105 (1858).

Aspidium tacticopterum Kunze in Linnaea 24 : 290 (1851).

Rhizome erect, scaly ; fronds tufted 60–90 cm long. Stipes about half as long as the lamina, densely scaly, the *basal scales* up to 30 × 10 mm, *lanceolate with black centres and pale brown margins*, those along the stipe varying from very broadly ovate with black centres to lanceolate and concolorous, both with long pointed apices and *mixed with copious, ferrugineous, linear to hair-like, pointed scales with strongly fimbriate margins. Lamina* 40–60 × 20–30 cm, oblong, *bipinnate*, grey-green in colour and cartilaginous in texture ; *main rhachis* densely scaly with narrow, attenuate, ferrugineous scales intermixed *with broad, thin, brown scales* : pinna rhachides clothed with narrow brown scales, becoming smoother distally ; pinnae subsessile, opposite or sub-opposite below, becoming alternate, patent or ascending, linear, acuminate, up to 15 × 2 cm, basal pair slightly reduced and sometimes deflexed ; *pinnules* 6–10 mm long, *shortly stalked*, becoming sessile then adnate distally, obliquely oblong-ovate, unequal at the base, posterior margin straight or narrowly cuneate, *anterior margin broadly truncate, subauriculate, margins spinulose serrate above, bluntly lobed below*, lowermost pinnule not or scarcely enlarged and often reduced on the lower pinnae ; under surfaces with scattered pale fibrils, becoming glabrous with age, upper surfaces glabrous. Sori situated about midway between the midribs and margins of the pinnules, few in number and often reduced or lacking on the posterior side ; *indusium absent* – in Ceylon specimens.

CEYLON : *Thwaites C.P. 3503* in part (K ; PDA). Frotoft jungle, *Freeman 216G* (BM). Ramboda Pass–Maturata track, in jungle, 1920 m, 17 March 1954, *Sledge 1307* (BM : K).

Forests of the Central Province at high elevations ; rare.

South India, Sikkim, Khasia.

Kunze described his species from South Indian specimens. It was not taken up by Hooker in the *Species Filicum,* was not even mentioned by Hooker and Baker in the *Synopsis Filicum,* and has been ignored by all later writers. Yet although Kunze admitted to having seen only a single frond he was in no doubt as to its being a very distinct species. I have examined the specimen in the Naturhistorisches Museum, Vienna, which is certainly authentic and presumably the type. This shows a fern which can readily be matched by sheets at Kew both from southern and northern India and also from Ceylon. The distinguishing characters are the grey-green or olive-green, bipinnate fronds with very numerous and regular, small pinnules, and the presence of broad scales on the main rhachis as well as narrowly linear to filiform scales. It is significant that Thwaites wrote on the label of the specimen sent to Kew, 'scales on the rhachis peculiar'. *P. yunnanense* Christ appears to be a very similar species, at least as construed by Christensen in *Contr. U.S. natn. Herb.* 26 : 286–287 (1931) though I have not seen authentic specimens.

Kunze's description says 'indusiis coriaceis, fuscis' but indusia are absent from most of the sori of the Vienna specimen. Ceylon specimens are exindusiate and so are most Indian specimens though indusia are sometimes present (e.g. *Gamble 7263* from Sikkim in Herb. Kew ; *Chandra 65536* from Shillong peak, Assam, in Nat. Bot. Gard., Lucknow), and a second sheet from the Vienna museum (India orient. leg *Wight*) has indusia present on most sori. In other respects Ceylon specimens match the Vienna type specimen perfectly. The absence of an indusium I regard as of little taxonomic significance since in other species of *Polystichum* (e.g. *P. auriculatum* and *P. anomalum*) indusia may or may not be present on fronds which are otherwise identical.

P. tacticopterum is evidently a rare species in Ceylon judging by the very few specimens seen in herbaria. Freeman's gathering and my own were both from the Nuwara Eliya district.

5. ***Polystichum biaristatum*** (Blume) T. Moore, Index Fil. : 86 (1858).

Aspidium biaristatum Blume, Enum. Pl. Jav. : 164 (1828).—Hook., Sp. Fil. 4 : 29 (1862).
Aspidium aculeatum var. *biaristatum* (Blume) C. B. Clarke in Trans. Linn. Soc. Lond., Ser. 2, Bot. 1 : 510 (1880).
Polystichum aculeatum var. *biaristatum* (Blume) Bedd., Handb. Ferns Brit. Ind. : 209 (1883).

Rhizome erect, scaly ; fronds tufted, up to 1 m long. Stipe about the same length as the lamina, very scaly, the *basal scales* up to 20 × 5 mm, lanceolate, attenuate, *with black centres and brown margins,* those along the stipe consisting of a mixture of lanceolate, finely pointed scales some with black centres and some brown and concolorous, and shorter, linear-lanceolate to filiform, hair-like scales with fimbriate margins. *Lamina* 45–65 × 20–30 cm, oblong-lanceolate or ovate-lanceolate, *bipinnate,* stiff and firm in texture ; *main rhachis with abundant, linear-lanceolate to filiform, brown scales with fimbriate bases,* usually intermixed especially in the lower part with dark scales like those of the stipe ; pinna rhachides similarly clothed with narrow, brown scales ; pinnae very shortly stalked, alternate, spaced (3–4 cm apart in the lower part of the frond), ascending and often falcate, oblong, acuminate, up to 15 × 3 cm ; *pinnules* 15–20 (30) mm, *rhombic-ovate,* or less commonly narrowly rhombic-lanceolate, unequally narrowed to the base, *posterior margin straight or narrowly cuneate, anterior margin broadly cuneate to truncate, obscurely auriculate* on the anterior base but sometimes with the auricle well developed, *very shortly stalked or subsessile,* becoming adnate distally, apex sharply acute or shortly aristate, often falcately curved, *margins usually serrate above* with acute or spinulose teeth, *subentire or dentate or shallowly lobed below* ; under surfaces with scattered hair-like scales on the veins, upper surfaces glabrous. Sori large, forming a line on either side of the midrib of each pinnule, either medially situated or frequently nearer the margin ; *indusium* circular, *peltate.*

CEYLON : *Thwaites C.P. 1367* (BM ; K ; PDA, Ramboda, Sept. 1847, *Gardner*). Nuwara Eliya, *Freeman 211B, 212C* (BM). Kikilimane, *Freeman 214E* (BM). Hakgala, *Freeman 219A* (BM). Oodawella, near Kandy, in jungle, 1230 m, 8 Dec. 1950, *Sledge 525* (BM). Adam's Peak, 1650 m, 14 Dec. 1950, *Sledge 606* (BM). Pedrotalagala, in shade, ca. 1800 m, 20 Dec. 1950, *Holttum 39191* (SING). Knuckles Mt., in forest, 1590 m, 30 Jan. 1954, *Sledge 1076* (BM). Above Le Vallon Estate, in forest, 1350 m, 9 Feb. 1954, *Sledge 1114* (BM). Tonacombe Estate, 1320 m, 21 Feb. 1954, *Sledge 1162* (BM). *Walker* (K). *Gardner 1099, 1100, 1101* (K). *Hooker f. & Thomson 292a* ex *Herb. J. Smith* (BM).

Common in the forests of the interior above 1200 m.

South India, Sikkim, Bhutan, Assam, S. China, Burma, Thailand, Java, Celebes, Formosa.

The type sheet of Blume's species carries one frond 45 cm long with most of the stipe absent, and the top part of a second frond. Despite the absence of all but the uppermost part of the stipe, the other characteristics which these fronds display leave little doubt that they represent the same species as many Ceylon specimens. Sometimes (*Sledge 1114, Holttum 39191*) the pinnules are narrowly and unequally rhombic-lanceolate (trullate) with narrowly cuneate bases, resembling those of *P. squarrosum* (Don) Fée. Similar plants occur in northern India, e.g. *Griffith* spec. from Bhutan and *Wenger* spec. from South Lushai det. *P. biaristatum* by Christensen, both in Herb. Kew.

This is the most common species of *Polystichum* in Ceylon. The large pinnules at once distinguish it from *P. tacticopterum* and *P. setiferum* var. *nigropaleaceum.* The former also differs in its olive-green or grey-green colour, more numerous pinnules and exindusiate sori ; the latter in its softer texture and aristate-serrate pinnules. *P. anomalum,* in which the pinnules are comparable in size with those of *P. biaristatum,* is readily separated by its exindusiate sori and its concolorous scales.

6. ***Polystichum setiferum*** (Forssk.) T. Moore ex Woynar in Mitt. naturw. Ver. Steiermark 49 : 181 (1913).

Polypodium setiferum Forssk., F. Aegypt.-Arab. : 185 (1775).

a. var. ***setiferum***

Not in Ceylon.

b. var. ***nigropaleaceum*** (Christ) Sledge, comb. nov.

Polystichum aculeatum var. *angulare* Bedd., Handb. Ferns Brit. Ind. : 207 (1883) pro parte, non *Aspidium angulare* Willd.
Polystichum aculeatum var. *nigropaleaceum* Christ in Ber. schweiz. bot. Ges. 3 : 38 (1893).
Polystichum nigropaleaceum (Christ) Diels in Naturl. PflFam. 1 (4) : 191 (1899).
Aspidium angulare sensu Hope in J. Bombay nat. Hist. Soc. 14 : 472 (1902) ; non Willd.
Polystichum fuscopaleaceum Alston in Bolm Soc. broteriana, Ser. 2, 30 : 22 (1956).
Polystichum setiferum var. *fuscopaleaceum* (Alston) Schelpe in Bolm Soc. broteriana, Ser. 2, 41 : 216 (1967).

Rhizome erect, scaly ; fronds tufted up to 90 cm long. Stipe half or more as long as the lamina, scaly with a mixture of broad, lanceolate, finely pointed *scales* 10 mm long *with dark castaneous to black centres and paler, fimbriate margins and filiform, hair-like, ferrugineous scales with strongly fimbriate bases*. *Lamina* 25–60 × 8–16 cm, oblong, *bipinnate, soft in texture* ; main rhachis shaggy, at least when young, with slender, ferrugineous, hair-like scales intermixed with some broader lanceolate-attenuate ones ; pinna rhachides similarly woolly with hair-like scales, becoming smoother distally ; pinnae very shortly stalked, opposite or sub-opposite below, becoming alternate, patent or ascending, linear, acute, up to 10 × 2 cm, basal pair not or slightly reduced ; *pinnules shortly stalked,* 6–10 mm long, obliquely ovate, obtusely angled and very unequal at the base, posterior margin cuneate, *anterior margin broadly truncate or rounded and auriculate,* acute or rounded at the *awned apex, serrate with setiform teeth along the margins* and awned at the apex of the auricle, basal acroscopic pinnules often enlarged, sometimes conspicuously so, and more lobed ; under surfaces with scattered fibrils, upper surfaces glabrous. Sori small, situated midway between the midrib and margin of the pinnules and terminal on acroscopic branch veins ; *indusium* circular, *peltate*.

CEYLON : *Thwaites C.P. 3503* in part (BM ; K ; PDA, Nuwara Eliya, April 1856, and Maturata 1857 ; 2100 m, fide BM and K sheets). Nuwara Eliya, *Freeman 211A* (BM). 'Comm. *G. Wall,* 1884, small form' (PDA).

Forests of the Central Province at high elevations ; rare.

South India (Nilgiri and Pulney Hills), Himalayan range from Kashmir to Khasia. Mountains of tropical Africa.

In the texture of the fronds and shape of the pinnules this seems to me to overlap completely with many European specimens of this variable species. The only difference I see is in the presence of some very dark-centred scales on the stipe. Hope (loc. cit. 473) also concluded 'I find I cannot definitely separate from *A. angulare* any of the Himalayan material which has been placed under that species'.

In his account of the forms of *P. aculeatum,* Christ used the names *P. lobatum* and *P. aculeatum* to refer to what are now called *P. aculeatum* and *P. setiferum* respectively. I have been unable to trace the type of his *P. aculeatum* var. *nigropaleaceum* which was described from north India and which was characterized by 'un duvet sur le rachis consistant d'écailles noires'. This would seem to be the best name for Ceylon plants although in them the dark-centred scales scarcely extend to the rhachis. In the absence of any detectable difference other than the scales between European and Ceylonese or Indian specimens, it seems best to retain the subordinate rank originally given to it. Schelpe (loc. cit.) has reached a similar conclusion about African plants which he names *P. setiferum* var. *fuscopaleaceum* (Alston) Schelpe, stating that African specimens with dark scales 'intergrade with the temperate or tropical high mountain forms with pale stipe scales to such an extent that a clear differentiation at specific level is not possible'. Since the dark scales provide the only means of distinguishing both African and Indian plants, the oldest name at varietal rank has priority.

Of Blume's numerous named species or forms this comes closest to *Aspidium microphyllum* which seems to me to be a form of *P. setiferum*. The type of that however does not show any dark scales. *Hooker fil. & Thomson 292* from Ceylon in Herb. Edin. – a large frond mounted on two sheets – is without dark scales but appears to be referable to *P. setiferum* agg.

This is evidently as rare a species in the mountains of southern India as in those of Ceylon. *Gamble 15316* from the Nilgiris and *Bourne 4907* from the Pulney Hills are typical examples ; but there is only one other gathering from South. India at Kew.

P. moluccense (Bl.) Moore (*P. horizontale* Presl).

A specimen of this very distinct species in Herb. Hooker at Kew, annotated by Hooker 'Ceylon. Mrs Gen^{l} Walker' probably originated from the Peradenyia Botanic Gardens. I have seen no other gathering from Ceylon.

4. ***ARACHNIODES*** Blume

ARACHNIODES Blume, Enum. Pl. Jav. : 241 (1828).

Rhizome usually creeping, rarely short and erect, scales entire or subentire, uniform ; fronds tripinnatifid to 5-pinnate, never simply pinnate, anadromic, broadly deltoid or pentagonal in outline and never bearing gemmiferous buds, coriaceous or herbaceous in texture, the lowermost pinnae often basiscopically enlarged and the pinnules or their segments commonly spinulose-serrate ; indusium orbicular with a deep sinus and overlapping lobes.

As described above this genus rests on a combination of characters ; no clear and consistently reliable single character exists whereby its species may be unfailingly distinguished from those of *Dryopteris* and *Polystichum*. Ching and Copeland (as *Rumohra*), Holttum (as *Polystichopsis*), Morton (as *Byrsopteris*), and Tindale (as *Arachniodes*) have all discussed this 'rather unsatisfactory genus' and Tindale's account (in *Contr. N.S.W. natn. Herb.* 3 : 89–90 (1961) ; *op. cit. Flora Series* 208–211 : 55–58 (1961)) should be referred to for its history.

As construed by Ching, *Rumohra* was compounded of *Arachniodes*, *Dryopteris*, *Polystichum*, and *Rumohra sensu stricto*. He considered it a synthetic group arrived at 'along two quite distinct evolutional lines, namely *Eudryopteris* and *Polystichum* respectively'. Copeland (*Gen. Fil.* : 113 (1947)) objected that 'A "genus" so derived would not be a genus at all' but expressed himself as satisfied with its naturalness. I do not share Copeland's satisfaction. Even after the removal of discordant species, its boundaries remain somewhat ill-defined though its maintenance seems to be justified if only on the grounds of convenience.

KEY TO SPECIES OF *ARACHNIODES*

Rhizome creeping :
  Frond with linear-elongate apical pinna similar to lateral ones immediately below it ; sori submarginal . . . . 1. *A. amabilis*
  Frond gradually attenuate above ; sori distant from margin . 2. *A. aristata*
Rhizome erect . . . . 3. *A. tripinnata*

1. **Arachniodes amabilis** (Blume) Tindale in Contr. N.S.W. natn. Herb. 3 : 90 (1961).

Aspidium amabile Blume, Enum. Pl. Jav. : 165 (1828).—Hook., Sp. Fil. 4 : 25, t. 225 (1862).
Lastrea amabilis (Blume) T. Moore, Index Fil. : 85 (1858).—Bedd., Ferns S. Ind. : 37, t. 109 (1863) ; Handb. Ferns Brit. Ind. : 228 (1883).
Polystichum amabile (Blume) J. Smith, Ferns Brit. & For. : 152 (1866).—C. Chr., Index Fil. : 578 (1906).
Rumohra amabilis (Blume) Ching in Sinensia, Shanghai 5 : 41 (1934).

Rhizome creeping, covered with lanceolate, attenuate, dark brown, entire scales up to 7 mm long. Stipes well spaced, about equalling the lamina, scaly below, becoming more or less glabrous above. *Lamina bipinnate*, oblong-ovate with up to 8 pairs of pinnae below the *apical part of the frond which itself resembles one of the lateral pinnae* ; the latter distant, up to 20 × 3·5 cm, stalked, acuminate, the basal pinnae somewhat larger and with the lowermost basiscopic pinnules enlarged, up to 7·5 cm, and pinnate ; pinnules shortly stalked, rhombic, 1·5–2 × 0·5–1·0 cm, posterior margin cut away, anterior base truncate, obscurely auriculate, margins spinulose-serrate or dentate or shallowly lobed with aristate tips to the teeth or lobes ; main rhachis and pinna rhachides with scattered, narrow, brown scales ; texture submembranaceous. *Sori submarginal*, indusia orbicular with a sinus, or sometimes peltate, dark brown, persistent.

CEYLON : *Thwaites C.P. 3287* (BM ; E ; K ; PDA, Ramboda Pass, Feb. 1854). Haputale Pass, Badulla, Feb. 1858, as *C.P. 3287* ex *Herb. Oswald Brodie* in *Herb. Neill Fraser* (E). Nuwara Eliya, *Freeman 223A, 224B* (BM). Hakgala, *Mrs Chevalier* (BM). Same locality, jungle below road, 23 May 1911, *J. M. Silva* (PDA). Same locality, by stream in jungle at 1650 m, 27 Dec. 1950, *Sledge 737* (BM). Same locality, 20 Feb. 1954, *Sledge 1157* (BM). Kandapola near Nuwara Eliya, in forest near Parawella Falls, 1425 m, 19 March 1954, *Sledge 1331* (BM ; K). *Ferguson* (PDA ; US *815347*). *Robinson 135* (K). *Trimen* ex *Herb. Beddome* (K). *Hance* ex *Thwaites* (BM). Hort. Kew ex Ceylon, 1858, 1859 ex *Herb. J. Smith* (BM). *Anderson* (E). *Wall* in *Herb. Neill Fraser* (E).

In forests in the more elevated parts of the Central Province.

South India (Nilgiri Hills and other elevated parts), Nepal, Assam, S. China (Yunnan, Szechwan, Kwangtung), Japan, Formosa, Philippines, Java.

2. ***Arachniodes aristata*** (Forst. f.) Tindale in Contr. N.S.W. natn. Herb. 3 : 89 (1961) ; op. cit., Flora Ser. 208–211 : 58 (1961).

Polypodium aristatum Forst. f., Florul. Ins. Austr. Prodr. : 82 (1786).
Aspidium aristatum (Forst. f.) Swartz in J. Bot. Göttingen 1800 (2) : 37 (1801).
Polystichum aristatum (Forst. f.) C. Presl, Tent. Pterid. : 83 (1836).—C. Chr., Index Fil. : 578 (1906).
Aspidium carvifolium Kunze in Bot. Ztg 6 : 283 (1848) '*curvifolium*' ; in Linnaea 24 : 292 (1851).
Lastrea aristata (Forst. f.) T. Moore, Index Fil. : 86 (1858).—Bedd., Ferns S. Ind. : 36, t. 101, excl. fig. A (1863) : Ferns Brit. Ind. : t. 261 fig. sinistr. sup. (1868) ; Handb. Ferns Brit. Ind. : 229 (1883).
Dryopteris aristata (Forst. f.) Kuntze, Rev. Gen. Pl. 2 : 812 (1891).
Rumohra aristata (Forst. f.) Ching in Sinensia, Shanghai 5 : 50 (1934).—Copel., Gen. Fil. : 113 (1947) ; Fern Fl. Philipp. : 252 (1960).
Polystichopsis aristata (Forst. f.) Holtt., Fl. Malaya 2 : 486 (1954).
Byrsopteris aristata (Forst. f.) C. V. Morton in Am. Fern. J. 50 : 152 (1960).

Rhizome long-creeping clothed with linear, acuminate, entire, dark-brown scales, 10 × 1 mm ; fronds spaced, up to 90 cm long. Stipes usually longer than the lamina, densely clothed towards the base with linear, dark brown, entire scales with more or less fimbriate bases, sparsely scaly above ; main rhachis and pinna rhachides similarly scaly. *Lamina* 20–40 × 15–25 cm, *tripinnate or quadripinnate below*, deltoid in outline, subcoriaceous in texture, with 5–6 pairs of stalked, ascending, well spaced pinnae below the pinnate and acuminate apical part of the frond ; basal pair of pinnae much the largest, up to 30 cm long with the lowermost basiscopic pinnules usually much enlarged (often over 10 cm long) and always pinnately divided, sometimes with its basal segments again almost or quite pinnate, the remaining pinnae below the simply pinnate and acuminate apex of the frond generally simply pinnate with the pinnules lobed or pinnatifid but with the acroscopic basal pinnules often again pinnate ; proximal pinnules stalked, becoming sessile then adnate distally, ovate-rhomboid or rhomboid-lanceolate, posterior base straight or narrowly cuneate, anterior base truncate and subauriculate, *apex aristate, margins spinulose serrate* or lobed or divided quite to the costa in the largest pinnules with the lobes spinulose serrate and aristate pointed ; under surfaces with scattered fibrils on the veins, upper surfaces glabrous and glossy. *Sori* in a single row on each side of the midrib of the segments and *closer to the midrib than to the margin*, terminal on the anterior veinlet or each group ; indusium orbicular, attached by a deep sinus, dark brown, more or less persistent.

CEYLON : *Thwaites C.P. 1373* partim (BM ; E). *Thwaites C.P. 3384* (BM ; K). *Thwaites C.P. 3937* (CGE ; E ; K ; PDA, Nuwara Eliya, 1847, *Gardner*). Forests on Hantane, July 1844 ; Elephant Plains, Oct. 1845, *Gardner 1098* (CGE ; K). Asgiria, Matale, 1860, as *C.P. 1373* ex *Herb. Oswald Brodie* in *Herb. Neill Fraser* (E).

Kandy, *Mrs Chevalier* (BM). Same locality, in jungle, 3 June 1927, *Alston 1094* (PDA). Same locality, 630 m, 12 Jan. 1954, *Schmid 850* (BM). Lady Horton's Walk, Kandy, 600 m, 7 Dec. 1950, *Sledge 502* (BM). Kandy Catchment, in secondary jungle, 750 m, 4 Feb. 1954, *Sledge 1097* (BM). Nuwara Eliya, *Freeman 225A* (BM). Hakgala, banks of stream in jungle, 28 Feb. 1906, *J. C. Willis* (PDA). Hakgala Heights, 1800 m, 16 Dec. 1950, *Sledge 629* (BM). Jungle at Le Vallon, Central Province, 1500 m, 9 Feb. 1954, *Sledge 1111* (BM). Jungle at Goussa, near Ella, 900 m, 21 Feb. 1954, *Sledge 1217* (BM). Lagalla, Matale East, May 1884, no collector's name (PDA). *Gardner 1373* (K). *Ferguson* (PDA ; US *815349*, *815477*). *Alex. Prior* (K). *Robinson* (K). *Walker* (K). 15 March 1819, *Moon 535* (BM). Hort. Kew, 1852, ex *Herb. J. Smith* (BM). *Wall* (E).

Common in forests from 500 to 2000 m.

South India, China, Japan, Korea southwards to Malesia and E. Australia (New South Wales and Queensland) and eastwards to Polynesia.

This is one of the commonest ferns of Ceylon. The differences between it and *A. tripinnata* are referred to under that species. Apart from the morphological differences the two species differ cytologically, *A. tripinnata* being diploid and *A. aristata* tetraploid.

According to Ching (*Acta bot. sin.* 10 : 256 (1962)) the continental Asiatic and Japanese plant is *Arachniodes exilis* (Hance) Ching, Forster's species being confined to N.E. Australia. No descriptions however are given by Ching nor any statement as to how they differ. Hance (*J. Bot., Lond.* 21 : 268 (1883)) compared his species, which was founded on a single imperfect specimen from Chekiang, with *Aspidium braunii*.

3. **Arachniodes tripinnata** (Goldm.) Sledge, comb. nov.

Polystichum tripinnatum Goldm. in Nova Acta Acad. Caesar Leop. Carol. 19, Suppl. 1 : 463 (1843).

? *Polystichum formosissimum* Goldm., loc. cit.

Lastrea coniifolia Bedd., Ferns Brit. Ind. : t. 261, excl. fig. sinistr. sup. (1868) pro parte, non *Aspidium coniifolium* Wall. ex Mett. ; Handb. Ferns Brit. Ind. : 230, fig. 118, excl. A (1883).

Polystichum carvifolium C. Chr., Index Fil. : 580 (1906) pro parte, non *Aspidium carvifolium* Kunze et excl. syn. *Aspidium coniifolium* Wall. ex Mett.

Dryopteris carvifolia sensu C. Chr. in Contr. U.S. natn. Herb. 26 : 282 (1931), non *Dryopteris carvifolia* (Kunze) C. Chr.

Rumohra carvifolia Ching in Sinensia, Shanghai 5 : 60 (1934) pro parte, non *Aspidium carvifolium* Kunze.—Copel., Fern Fl. Philipp. : 253 (1960).

Arachniodes carvifolia Ching in Acta bot. sin. 10 : 256 (1962) pro parte, non *Aspidium carvifolium* Kunze.

Differs from *A. aristata* in its *erect rhizome* with clustered and often larger fronds up to 1·5 m long, in the *broader lanceolate scales* at the base of the stipe and in the *teeth of the pinnules and pinnule segments* being either bluntly or acutely serrate but *not aristate pointed* and in its smaller and more fugaceous indusium.

CEYLON : *Thwaites C.P. 3938* (CGE ; E ; K ; PDA). *Thwaites C.P. 1373 partim* (E ; K). Adam's Peak, in forests, March 1846, *Gardner* (CGE). Same locality, 5 Jan. 1951, leg. *I. Manton, Sledge 825* (BM). Kotmalee, 1847, *Fortescue* (CGE). Nuwara Eliya, *Mrs Chevalier* (BM). Hakgala, by track in jungle, 1650 m, 23 Dec. 1950, *Sledge 709* (BM). Corbet's Gap, amongst rocks in secondary jungle, 1320 m, 9 Dec. 1950, *Sledge 559* (BM). Nawanagalla, west of Madugoda, in jungle, 1110 m, 8 Jan. 1954, *Sledge 938* (BM). Ambagamuwa, 570 m, 19 Jan. 1954, *Sledge 996* (BM). Gongalla Hill, in jungle, 1150 m, 11 March 1954, *Sledge 1292* (BM). Forest at Beverley Estate, Deniyaya, 780 m, 4 March 1954, *Sledge 1398* (BM). 1847, *Gardner 1098* (E). 30 Jan. 1819, *Moon 57* (BM). *Mrs Walker* (K). *Hooker f. & Thomson 273* ex *Herb. J. Smith* (BM). Hort. Kew, 1860, 1862 ex *Herb. J. Smith* (BM). *Ferguson* (PDA ; US *815352*). *Anderson* (E). *Wall* (E) ex *Herb. Oswald Brodie* in *Herb. Neill Fraser* as *C.P. 1373* (E). *Palliser* (US *683988*).

Common in forests of the interior.

South India, Java, Sarawak, Philippines.

This is usually – though not invariably – a larger, coarser plant than *A. aristata* from which it is easily distinguished in the field by its very different habit. Herbarium specimens lacking rhizomes but with the base of the stipe intact can be distinguished by the decidedly broader basal scales. The pinnules are often bluntly serrate and though the teeth may be sharply pointed they do not ever appear, at least in Ceylon specimens, to be aristate. The indusium also is smaller and more fugaceous in *A. tripinnata* and sometimes the sori are exindusiate. According to Ching's key (*Sinensia, Shanghai* 5 : 38, 1934) the sori are said to be 'dorsal on veinlets', but this is not so ; they are terminal in position as in *A. aristata*.

The present species is widespread in South India and Ceylon and has long been erroneously referred to Kunze's *Aspidium carvifolium*. Kunze's description, based on fronds lacking the basal part of the stipe and rhizome, refers to the pinnules as 'versus apicem aristato-dentatis' which is one of the characters distinguishing *A. aristata* from the present species. He quoted *Hohenacker 905* and *Cuming 262* as examples of his species and sheets of both these collections in Herb. Kew (also *Hohenacker 905* in Herb. BM) represent *A. aristata*. The Kew sheet of Cuming's collection moreover shows the creeping rhizome. There is also in Herb. Kew a specimen sent to Hooker by Reichenbach fil. as *A. carvifolium* Kunze and annotated by the sender 'compared with the types'. This specimen was collected in the Nilgiri Hills by Schmid, on whose collections from here Kunze founded his species, and this specimen also represents *A. aristata*. As there is moreover no reference anywhere in Kunze's paper on Nilgiri ferns to *A. aristata* it is evident that his *A. carvifolium* was a redescription of Forster's species.

The type of Goldmann's *Polystichum tripinnatum*, described from a Manila specimen collected by Meyen, is at Berlin. It consists of a lamina only. Several gatherings from the Philippines (e.g. *Elmer 9949, 17844*) labelled *P. carvifolium* match the Goldmann sheet tolerably well. Another specimen of Meyen's collection from Manila labelled *Polypodium/Aspidium aristatum* does not differ significantly from Goldmann's species whilst *P. formosissimum* Goldm. could well again be a less divided example of the same species. It is certainly a better match for some other Philippine specimens labelled *P. carvifolium* than for authentic *A. aristata* with which it has been equated by Christensen.

In the *Index Filicum* Christensen cites *P. tripinnatum* Goldm. as synonymous with *P. carvifolium* (Kunze) C. Chr. and it is not clear why the latter was treated as the valid name when the former had priority of publication. Subsequent authors have followed Christensen and ignored Goldmann's name. Though I am quite sure that the name *Aspidium carvifolium* Kunze cannot be used for the species under consideration, I am less sure that Ceylon plants are identical with Goldmann's *P. tripinnatum.* At least we know however from matching Philippine specimens that Goldmann's type in all probability had an erect rhizome. But the form of the frond and the size and shape of the pinnules seem to me to be closer to the type specimen of Blume's *Arachniodes aspidioides.* The latter has been regarded as the same as *Aspidium pulchellum* Blume which Rosenstock reduced to a variety of *A. aristata.* But we do not know if these Blume species had erect or creeping rhizomes. Unfortunately all Meyen's and Blume's specimens are devoid of rhizomes and the basal parts of the stipes and hence are inadequate for firm determinations in a group where habit is of primary importance. I do not believe that bipinnate or tripinnate division of the fronds is of more than minor taxonomic significance in this group and pinnule form is also prone to considerable variation in different populations of the same species. I suspect that the Ceylon species may be distinct from the Philippine one and the latter may be the same as *Arachniodes aspidioides* but it seems best to retain Goldmann's epithet for the present to cover the species currently but mistakenly called *Arachniodes carvifolia* until more information is available which will enable a decision to be reached as to whether *A. aspidioides* is a distinct species and if so what its relationship is with Philippine and Ceylonese plants. At present this can only be a matter of conjecture.

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NEW HIMALAYAN AND TIBETAN SPECIES OF *CORYDALIS* (PAPAVERACEAE)

F. LUDLOW
AND
W. T. STEARN

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BY

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Pp. 45-69; 15 *Plates*; 14 *Text-figures*

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NEW HIMALAYAN AND TIBETAN SPECIES OF *CORYDALIS* (PAPAVERACEAE)

By FRANK LUDLOW* AND WILLIAM T. STEARN

SUMMARY

The genus *Corydalis* reaches its greatest morphological diversity and has its greatest concentration of species, probably 150 to 200, in the Sino-Himalayan region. This paper describes and illustrates ten new species from Nepal, Bhutan and Assam and five from Tibet ; one (*C. ludlowii*) is unique within the genus in having undivided leaves. The 30 species now known from Nepal are listed. The specimens cited are all in the Herbarium of the British Museum (Natural History), London.

HISTORICAL INTRODUCTION

THE genus *Corydalis* Vent. attains its greatest morphological diversity and has its greatest concentration of species in south-eastern Asia, notably in the Himalayan chain and western China. Whereas Europe, as recorded in the *Flora Europaea,* 1 : 252–254 (1964), possesses only 14 species (or at most 20) and North America, according to the monograph by Gerald Ownbey (Ann. Mo. bot. Gdn, 34 : 187–259 (1947)), only ten species (or at most 18), there are probably 150 to 200 in the Sino-Himalayan region. Its richness gradually became apparent during the last quarter of the nineteenth century. Thus in 1886 Forbes and Hemsley (J. Linn. Soc., Bot. 23 : 36–39 (1886)) listed 20 species of *Corydalis* from the whole of China, together with Korea. In 1889, however, Franchet, using the collections made by the French missionary Delavay, listed 17 species from Yunnan and Szechwan in his *Plantae Delavayanae* : 44–51, t.13–15 (1889). About the same time Maximowicz, using the collections made by the Russian explorers Potanin and Przewalski, described 19 species, 15 being new, from Kansu and adjacent Tibet, together with one new species from the western Himalaya, in his *Flora Tangutica* : 37–53, t.10–11 (1889). Earlier J. D. Hooker had described 24 Indian species, mostly collected in Kashmir, Kumaon and Sikkim, for Nepal was then virtually unknown, in the *Flora of British India,* 1 : 121–127 (1872). Further collecting enabled Prain to enumerate 52 Indian species, for which he helpfully provided a key (J. Asiat. Soc. Beng. 65(2) : 14–41 (1896)), together with three new Chinese species. In 1931 Handel-Mazzetti listed 42 species from Central and Western China in his *Symbolae Sinicae,* 7 : 338–355 (1931), which is primarily concerned with his own collections made on the 1914–18 Expedition to south-western China of the Akademie der Wissenschaften in Wien and does not attempt a comprehensive enumeration, still less a monographic survey.

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* Frank Ludlow, who died on 25 March 1972, devoted many years to the study of the genus *Corydalis.* He determined as new the Himalayan and Tibetan species described here and prepared descriptions in English. W. T. Stearn, working closely with Ludlow and examining the material with him, then translated these into Latin, prepared the account of *Corydalis ludlowii* and wrote the introduction – *Editor.*

This was a task undertaken by Friedrich K. G. Fedde (1873–1942). Having monographed the *Papaveraceae* subfamilies *Hypecoideae* and *Papaveroideae* in Engler's *Das Pflanzenreich*, IV.104 (1909), he then tackled the subfamily *Fumarioideae*, of which *Corydalis* is the largest genus, and from 1912 to 1936 he published in his *Repertorium Specierum Novarum*, a series of papers describing new species, mostly from China, and providing further information about others already published. Fedde never managed to complete his work. He did, however, publish a concise general survey, dividing the genus into sections and subsections, in *Die natürlichen Pflanzenfamilien*, 2 Aufl., 17b : 123–136 (1936). He there estimated the genus *Corydalis* as comprising about 300 species. A key by Stearn to 33 species which are or have been cultivated will be found in the Royal Horticultural Society's *Supplement to the Dictionary of Gardening* : 187–188 (1956) ; ed. 2 : 246–247 (1969), with one additional species included in ed. 2.

During their expeditions from 1933 to 1949 in the Himalaya and adjacent Tibet, of which an account will be found in the *Journal of the Royal Horticultural Society* 93 : 11–19 (1968), Frank Ludlow (1885–1972) and George Sherriff (1898–1967) collected many specimens of *Corydalis*, which in a living state are very attractive little plants and which in the herbarium present a challenging range of taxonomic problems. The Nepal collections of Polunin, Stainton, Sykes and Williams made from 1949 onwards also include many specimens of *Corydalis*. Prolonged study of this and the other material in the British Museum (Natural History), Kew and Edinburgh herbaria has made evident the existence of some 15 undescribed species. These are dealt with below. Numerous as these novelties are, there can be no doubt that many still remain to be discovered, especially in the area eastward from the great bend of the Tsangpo river. The drawings of floral details have been made by Mr Derrick Erasmus and Miss Victoria Goaman. It is hoped that these records will lighten the work of a younger botanist undertaking the formidable but fascinating and rewarding task of monographing this large and intricate genus.

SPECIES OF NEPAL

Hooker in 1872 recorded only one species of *Corydalis* definitely from Nepal, i.e. *C. juncea*, and five others by inference, since their ranges were stated to extend from Sikkim to Garhwal, Kumaon or Kashmir, i.e. *C. cashmeriana*, *C. chaerophylla*, *C. meifolia*, *C. ramosa* and *C. sibirica*. At least 30 species are now known from Nepal, with enough collections made to indicate their general distributional patterns, largely as a result of collecting since 1949. Some, such as *C. cashmeriana*, *C. govaniana*, *C. lathyroides*, *C. leptocarpa*, *C. polygalina* and *C. ramosa*, have long been known from outside Nepal ; some others, such as *C. chaerophylla*, *C. juncea* and *C. meifolia*, first described from Nepal, extend beyond it ; there remain, however, a relatively large number of species which appear to be endemic, e.g. *C. alburyi*, *C. clavibracteata*, *C. megacalyx*, *C. pseudojuncea*, *C. staintonii* and *C. sykesii*. The species recorded from Nepal previously or in this paper, with their dates of publication, are as follows : *C. alburyi* Ludlow, sp. nov. ; *C. cashmeriana* Royle (1833) ; *C. casimiriana* Duthie & Prain (1897) ; *C. chaerophylla* DC. (1824) ; *C. chasmophila*

Ludlow, sp. nov. ; *C. clavibracteata* Ludlow, sp. nov. ; *C. diphylla* Wall. (1826) ; *C. elegans* Wall. ex Hook. f. & Thoms. (1855) ; *C. flabellata* Edgew. (1851) ; *C. flaccida* Hook. f. & Thoms. (1855) ; *C. geraniifolia* Hook. f. & Thoms. (1855) ; *C. gerdae* Fedde (1922), syn. *C. mitae* Kitamura (1955) ; *C. govaniana* Wall. (1826) ; *C. hendersonii* Hemsl. (1894), syn. *C. nepalensis* Kitamura (1955) ; *C. hookeri* Prain (1896) ; *C. juncea* Wall. (1826) ; *C. lathyroides* Prain (1896) ; *C. latiflora* Hook. f. & Thoms. (1855) ; *C. leptocarpa* Hook. f. & Thoms. (1855) ; *C. longipes* DC. (1824) ; *C. megacalyx* Ludlow, sp. nov. ; *C. meifolia* Wall. (1826) ; *C. nana* Royle (1833) ; *C. polygalina* Hook. f. & Thoms. (1855) ; *C. pseudojuncea* Ludlow, sp. nov. ; *C. ramosa* Wall. ex. Hook. f. & Thoms. (1855) ; *C. staintonii* Ludlow, sp. nov. ; *C. stricta* Stephan ex DC. (1821), syn. *C. schlagintweitii* Fedde (1914) ; *C. sykesii* Ludlow, sp. nov. ; *C. trifoliolata* Franch. (1886).

FLORAL STRUCTURE AND TERMINOLOGY

The flower (labelled *a* in the accompanying text-figures) of *Corydalis* is zygomorphic and usually more or less horizontally poised ; it has two sepals and four petals so closely overlapping as to enclose completely the androecium and gynoecium. The two sepals (labelled *b* in the text-figures) are small and inconspicuous and often fall early. The uppermost petal of the horizontal corolla is termed the *petalum posticum* (labelled *c*) as it would be at the back or nearest the axis if the corolla were held vertically ; it is prolonged basally into a nectar-holding spur (*calcar*). The lowermost petal is termed the *petalum anticum* (labelled *d*) as it would be then at the front or remote from the axis ; often it has a basal swelling or gibbosity corresponding to the spur of the upper petal. Parallel with these, between them and partly covered by them, are the two *petala interiora* (labelled *e*). The androecium consists of two opposite stamen-sets or phalanges termed *synandria* or simply *stamina* (labelled *f*), each having a flattened blade formed of united filaments terminated by a central dithecous anther (i.e. with two anther-sacs or loculi) with a monothecous anther (i.e. with one anther-sac) on each side. A discussion of the morphological interpretation of the androecium in the *Fumarioideae* by Agnes Arber will be found in *New Phytologist*, 30 : 317–354 (1931) ; she here accepted Čelakovsky's view that the androecium consists of six stamens fused into two groups of three. The gynoecium (labelled *g*) ends in a stigma (labelled *h*) which provides important taxonomic characters. These floral characters are discussed in the course of a well-illustrated paper by Måns Ryberg in *Acta Horti Bergiani*, 19 : 175–191 (1960).

W. T. Stearn

DESCRIPTION OF NEW SPECIES

Corydalis alburyi Ludlow, sp. nov. (Plate 1)

Radix elongatus, interdum ramosus, 30 cm vel ultra longus, 1 cm crassus. *Caules* erecti, 10–15 cm alti, basi tantum 1 mm lati, superne ad 3 mm lati, partim in scritho obruti. *Folia basalia* pauca (1–3), 10–15 cm longa (petiolo 8–12 cm longo incluso), caules aequantia ; lamina tripartita, 2–3 cm longa, 3–5 cm lata, purpurea vel griseo-viridia, foliolis 3 profunde trilobatis, lobis obovatis integris 1·5–2 cm longis, 0·75–1 cm latis, petiolulis 3–8 mm longis ; *folium caulinum* nullum vel unicum paulo infra inflorescentiam positum et quoad magnitudinem formamque bracteae infimae simile, trilobatum, ad 3 cm longum (petiolo valido 1 cm longo incluso). *Inflorescentia* terminalis, racemosa, congesta. *Bracteae* (praeter infimam folii caulini similem) lobatae, sed vix manifestae. *Flores* 3–4, 'griseo-malvini' (fide Stainton), 'partim pallide ardisiaci, partim albidi' (fide G. F. Smith) ; pedicelli 15 mm longi, apice incrassati. *Sepala* minuta, dentata, 1 mm longa. *Petalum posticum* ad 22 mm longum (calcari 4·5 mm longo incluso), crista brevi, glande nectarifera 3 mm longa ; *petalum anticum* 15 mm longum, crista crassa brevi ; *petala interiora* 15 mm longa (ungue 7 mm longa incluso). *Stylus* 4 mm longus, basi incrassatus ; *stigma* vix visibile. *Capsula* (immatura) elliptica, 10 mm longa, 4·5 mm lata ; *semina* biseriata, 8, nigra, nitida, orbiculata, carunculo magno.

NEPAL : Dolpo Distr. pass between Chharka and Sangdah (28°50′N, 83°30′E), 5000 m, 'On scree. Leaves purple. Flowers greyish mauve', 23 July 1966, *Stainton 5571* (holotype in Herb. Brit. Mus.). 'Hidden Valley', 6 miles NNE of Dhaulagiri (28°47′N, 83°32′E), 5000 m, 13 June 1970, *Smith & Albury* (Photograph only).

When fruiting material is available this very remarkable species may possibly be assigned to Section *Oocapnos* Popov, a section characterized by its strongly inflated capsules. The immature elliptic capsule, with its short style, large black carunculate seeds, and elongate placentae, is strikingly like the immature capsule of *C. crassissima* Cambess. (*C. crassifolia* Royle). Of the five species included in the Section *Oocapnos* the present species seems to come nearest to *C. retingensis* Ludlow (*Bot. Notiser* 121 : 278 (1968)). It has the same stout pedicels swollen at the apex, the same simple stems gradually increasing in thickness from base to apex, similar congested racemes, purple-tinged leaves, thick coriaceous bracts, dull-coloured short-spurred flowers. The main distinction lies in their foliage, the ternate leaves of the present species contrasting with the pinnate leaves of the Tibetan plant. Both species grow in scree at high altitudes. First found by Mr J. D. A. Stainton in July 1966 the present species was re-discovered by Dr G. F. Smith and Mr S. D. Albury in June 1970 in a valley not far distant from Stainton's locality. Dr Smith writes : 'We found it 5–6 miles NNE of Dhaulagiri at between 16 000 and 17 000 feet on sloping static apparently humus-free detritus, and on steep unconsolidated scree . . . growing as solitary plants with no obvious association with any other species. On June 8th to 12th, 1970, it was just putting out its leaves at ground level on WNW facing slopes and was in flower on ESE facing slopes. Even in flower it did not seem to rise much above the general level of the scree surface. The leaves are grey green and remarkably flat in appearance. The flowers are about 2 cm long and are unevenly coloured, being pale slaty blue in parts, shading off to whitish over the main part of the corolla. A special feature is a pair of green oblong depressions on the lip of each petal near the tip. The plant has a tap root more than 2 feet long.'

The specific name commemorates Sydney Albury whose sudden and tragic death occurred in Nepal on the very afternoon he was engaged in collecting specimens.

Corydalis aurantiaca Ludlow, sp. nov. (Plate 2 ; Text-fig. 1)

Affinis *Corydalis latiflorae* Hook. f. & Thoms. et *C. gerdae* Fedde sed floribus magnis aureis insignis.

Herba perennis glabra 10–18 cm alta. *Radix* usque ad 15 cm longa, 3–5 mm crassa, apice residuis vaginantibus petiolorum emortuorum coronata. *Caules* 1–3, simplices vel raro ramosi, 6–12 cm alti, praeter par foliorum oppositorum bipinnatorum nudi. *Folia basalia* numerosa ; petioli 8–12 cm longi ; laminae quoad ambitum oblongae, 2–4 cm longae, 1–2 cm latae ; pinnae 2–4, oppositae, suboppositae vel alternae, 0·5–1·5 cm longae (petiolulo 2–6 mm longo incluso) ; pinnulae 3- vel 4-segmentatae, lobulis obovatis vel oblanceolatis obtusis. *Folia caulina* 2, opposita, basalibus similia sed minora, supra vel infra medium caulis posita. *Inflorescentia* racemosa, congesta, subumbellata, 4–6-flora ; pedicelli bracteas aequantes vel eis parum longiores. *Bracteae* 1–2 cm longae, antice palmatifido-lobatae, basi dilatatae cuneatae. *Flores* erecti. *Sepala* 1·5 mm longa, 2 mm lata, lacerata. *Petala* aurea ; posticum 20–21 mm longum (calcari curvato obtuso 3·5–4·5 mm longo incluso), lamina 16–17 mm longa, 4–5 mm lata, glande nectarifera 2 mm longa, cucullo cristato submucronulato, 5-venosa ; petalum anticum 15 mm longum cristatum. Phalanges 10–12 mm longae, 3-venosae. *Ovarium* immaturum 8 mm longum, 1·5 mm latum, ovulis biseriatis. *Stylus* 4 mm longus ; stigma bilobatum, processibus posterioribus eminentibus. *Capsula* ignota.

Bhutan : Saga La, Upper Mangde Chu, 4725 m, 14 July 1949, *Ludlow, Sherriff & Hicks 16830* (holotype in Herb. Brit. Mus.). Waitang, Tsampa, 4525 m, 18 June

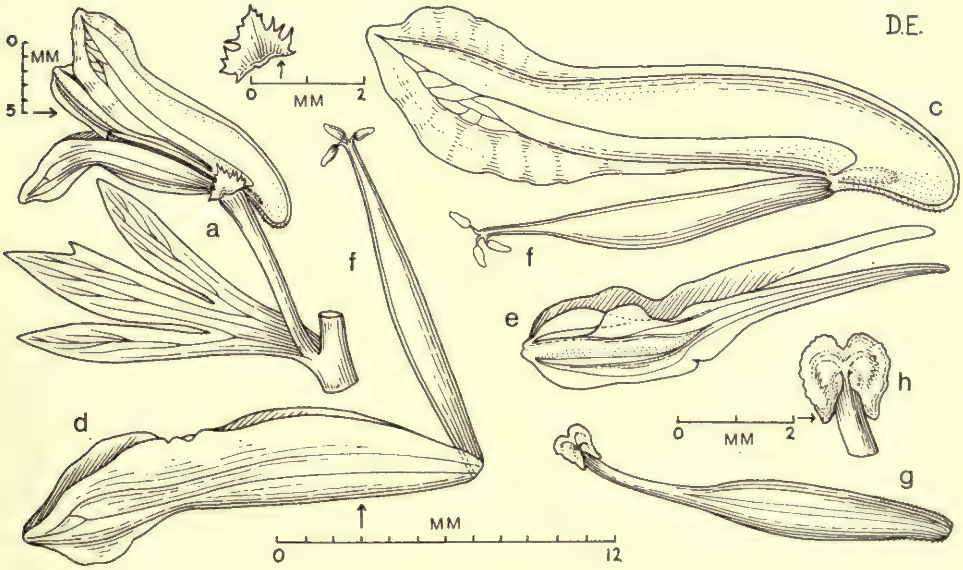


Fig. 1. *Corydalis aurantiaca* Ludlow : a, flower with bract and sepal ; c, posticous petal ; d, anticous petal ; e, inner petals ; f, phalange with anthers ; g, gynoecium ; h, stigma (*Ludlow, Sherriff & Hicks 16830*).

1949, *Ludlow, Sherriff & Hicks 19182.* Waitang, Tsampa, 4725 m, 22 June 1949, *Ludlow, Sherriff & Hicks 19224.* Marlung, Tsampa, 4725 m, 11 July 1949, *Ludlow, Sherriff & Hicks 19403.* Dole La, Bumthang, 4575 m, 22 June 1915, *Cooper 4033.* Bumthang, Dhur Chu, 4600 m, 8 June 1966, *Bowes Lyon 3409.*

This new species occurs in Central Bhutan and, so far, has not been recorded elsewhere. It is closely allied to *Corydalis latiflora* Hook. f. & Thoms. and *Corydalis gerdae* Fedde. All three species are of similar size and inhabit sandy scree or cliffs at high altitudes and possess long rhizomes from which arise one or more stems bearing a pair of opposite leaves. In all three species the inflorescence is subumbellate, with 4–10 flowers, which are broad and have a very short spur only ¼th or ⅕th of the length of the corolla. *C. aurantiaca* may be distinguished at a glance by its large golden-yellow flowers, those of the other two species being mauve or some shade of blue. *Corydalis mitae* Kitamura, *Fauna & Flora Nepal Himal.* : 275 (1955) seems indistinguishable from *C. gerdae* Fedde.

Corydalis chasmophila Ludlow, sp. nov. (Plate 3 ; Text-fig. 2)

Herba perennis, caespitosa, glabra. *Radix* validus ad 2 cm crassus, apice reliquiis lignosis petiolorum dense vestitus. *Caules* 5–7 cm alti, simplices. *Folia* omnia basalia, numerosa, ad 10 cm longa (petiolo ad 4 cm longo incluso) ; lamina pinnata, pinnis utroque latere rhachidis tenuis 2–3, oppositis suboppositis vel alternis, pinnatisectis, infimis petiolulis ad 4 mm longis instructis, summis subsessilibus vel sessilibus, lobis obovatis vel oblanceolatis obtusis. *Inflorescentia* racemosa, 3–12-flora ; pedicelli 40 mm (infimus) ad 5 mm (summus) longi, bracteis plerumque paulo longiores. *Bracteae* basi cuneatim expansae ; infima ad 5 cm longa, pinnata,

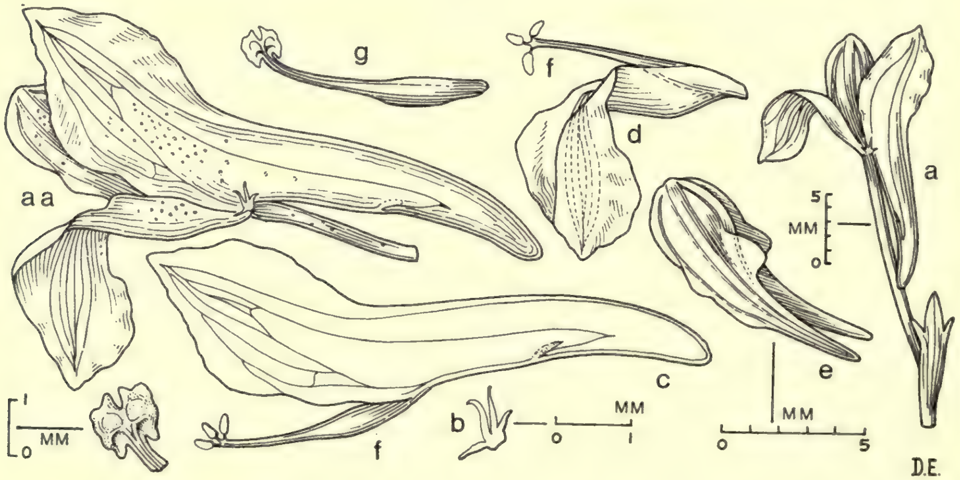


FIG. 2. *Corydalis chasmophila* Ludlow : a, flower with bract ; aa, flower ; b, sepal ; c, posticous petal ; d, anticous petal ; e, inner petals ; f, phalange with anthers ; g, gynoecium ; h (lowest left fig.), stigma (*Stainton 5408*).

pinnis utroque latere rhachidis latae 2–3, tri- vel bi-lobatis vel etiam summis integris, proxima ad 2 cm longa, pinnatisecta, lobis linearibus acutis, ceterae sursum decrescentes, infima harum palmatisecta, aliae tri- vel bi-secta, lobis linearibus acutis ad 4 mm longis. *Flores* flavi. *Sepala* minuta, laciniata, 0·75 mm diam. *Petalum posticum* ad 20 mm longum (calcari incluso); calcar rectum, angustatum, valde cristatum, glande nectarifera 5 mm longa; *petalum anticum* 10–11 mm longum, cristatum. *Stamina* 9 mm longa, dimidio basali expanso, vena mediana manifesta percursa. *Ovarium* immaturum 6 mm longum, 1·5 mm latum; *stylus* 2·5 mm longus; stigma late rectangularis papillis anterioribus 2, cornubus posterioribus 2.

NEPAL: Jangla Bhanjyang (28°50′N, 82°57′E), 3960 m, 'On limestone rocks, roots wedged deep in crevices', 30 May 1966, *Stainton 5408* (holotype in Herb. Brit. Mus.). Dojam Khola (29°06′N, 82°54′E), 5000 m, 5 July 1952, *Polunin, Sykes & Williams 63*.

BHUTAN: Black Mountain (27°17′N, 90°24′E), 4400 m, 'Growing in deep clefts in cliff face', 17 June 1937, *Ludlow & Sherriff 3269*.

This new species is closely allied to *Corydalis sykesii* Ludlow, from which it differs primarily in its smaller flowers. It is also allied, though less closely, to *Corydalis staintonii* Ludlow. All three possess many features in common. For example, all have an elongate rootstock capable of penetrating deeply into the fissures and crevices of the rocks and cliffs where they live. This rootstock is crowned with dense tufts of the vaginate bases of old lignified petioles from the centre of which arise the numerous flowering stems and radical leaves of the current year. Cauline leaves are absent, and the short unbranched flowering stems carry an inflorescence of 3–20 yellow flowers borne on long pedicels. The flowers, though differing in size, are similarly constructed. Both outer petals are crested, the spur is well developed and as long as or even longer than the rest of the petal, and the stigmas are similar, being broadly rectangular or almost circular with a prominent pair of anterior papillae and a posterior pair of horn-like processes.

Corydalis clavibracteata Ludlow, sp. nov. (Plate 4; Text-fig. 3)

Herba humilis, caespitosa, glauca, 8–12 cm alta. *Caudex* elongatus, c. 30 cm longus, reliquiis foliorum marcidis coronatus. *Folia basalia* numerosa, petiolata (petiolis complanatis 3–6 cm longis 2–3 mm latis), 6–12 cm longa, caulibus floriferis longiora, pinnatim 2–4 jugata, quoad ambitum anguste oblonga, pinnis imbricatis vel late oblonga pinnis discretis; pinnae alternae vel suboppositae petiolulatae, iterum pinnatim divisae; pinnulae petiolulatae; lobuli ultimi lineari-lanceolatis acuti. *Folia caulina* basalibus similia. *Inflorescentia* racemosa, congesta, 15–20-flora, foliis basalibus partim occulta. *Bracteae* clavatae, erectae, apiculatae, usque ad 2 cm longae, pedicellos aequantes, integrae vel apice lobatae. *Sepala* persistentia, 2 mm longa, longe dentata. *Petala* lutea, posticum 14–16 mm longum (calcari 7–8 mm longo incluso), crista brevi calcari non attingenti, glande nectarifera 5 mm longa; anticum 7–8 mm longum; interiora 6 mm longa, ungue 2–5 mm longo.

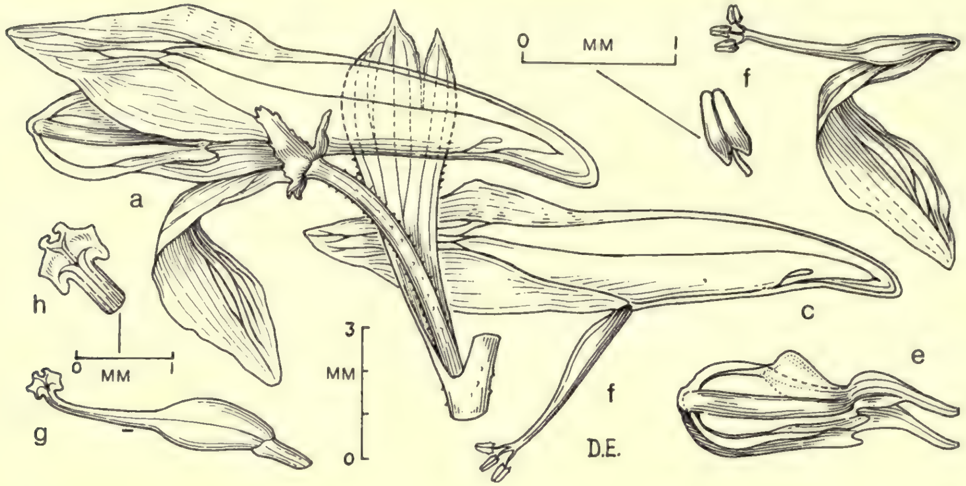


FIG. 3. *Corydalis clavibracteata* Ludlow: a, flower with bract; c, posticous petal; d (top right fig.), anticous petal; e, inner petals; f, phalange with anthers; g, gynoecium; h, stigma (*Polunin, Sykes & Williams 3540*).

Stylus 2 mm longus; stigma rectangulare. *Capsula* valde reflexa, oblonga, 3–5-seminalis. *Semina* rotundata, nigra, nitida, c. 1·25 mm diametro.

NEPAL: Ringmigaon, Phoksumdo Tal, slopes of Kanjiroba (29°04′N, 82°56′E), 4700 m, 'Leaves glaucous green. Perianth yellow flushed brown', 21 Sept. 1952, *Polunin, Sykes & Williams 3540* (holotype in Herb. Brit. Mus.). Near Balangra Pass (29°05′N, 82°41′E), 4500 m, 'Foliage glaucous. Wet places in exposed soil near snow and melting streams', 27 July 1952, *Polunin, Sykes & Williams 2595*. Phoksumdo Tal (29°05′N, 82°57′E), 3660 m, 'On streamside gravel, leaves grey, fleshy, flowers yellow with black blotch', 11 July 1966, *Stainton 5509*. Same locality, 'On scree, leaves grey, flowers yellow with brown blotch', 11 July 1966, *Stainton 5511*.

This new species belongs to Subsection *Mucroniferae* Fedde. It can readily be distinguished from other species in the subsection by its bracts, which in outline are shaped like an Indian club. Sometimes all bracts are entire but more often the lower are lobed at the apex. As its long tap root indicates, this is a scree or gravel plant. It resembles *C. megacalyx* Ludlow very closely but has totally different bracts.

Corydalis fimbripetala Ludlow, sp. nov. (Plate 5; Text-fig. 4)

Species *C. mucroniferae* Maxim. affinis sed bracteis anguste petiolatis et petalo antico fimbriato facile distinguenda.

Herba perennis, glabra, 4–8 cm alta. *Radix* perpendicularis, cylindrica, ad 10 cm longa, 3 mm diam. *Caulis* ramosus, primo brevis et foliis fere occultus, demum manifestus. *Folia* numerosa, 3–6 cm longa (petiolo 2–4 cm longo incluso); lamina

trisecta vel jugatim pinnata, segmentis bi- vel tri-partitis breviter petiolulatis vel subsessilibus lobis oblongis vel obovatis c. 0·5–1·5 mm latis. *Inflorescentia* diffusa e racemis numerosis brevibus composita ; pedicelli filiformes, c. 4–12 mm longi. *Bracteae* infimae foliaceae ternatim dissectae, ad 12 mm longae, superiores minores tantum apice trisecta, ad 8 mm longae, omnes longe petiolata, petiolis tantum 0·3–0·5 mm latis. *Flores* congesti, erecti, sordide flavi. *Sepala* squamiformia, 1 mm diam., integra vel leviter dentata. *Petalum posticum* c. 15 mm longum (calcari incluso) ; calcar anguste cylindricum, 7·5 mm longum, 0·75 mm latum, apice parum saccatum, glande nectarifera 5–6 mm longa apicem calcaris paene attingente ; lamina breviter cristata ; *petalum anticum* 9 mm longum, lamina c. 4 mm longa, 3·5 mm lata, margine valde fimbriata, in unguem c. 2 mm latum transienti, *Ovarium* peranguste obovoideum, ovulis 5–6 ; stylus gracilis ; stigma papillis 6. *Capsula* immatura elliptica, c. 4 mm longum, 2 mm latum.

Tibet : Reting, 60 miles N of Lhasa (30°22′N, 91°28′E), 4900 m, 28 July 1942, *Ludlow & Sherriff 8910*. Reting, 4400 m, 30 July 1944, *Ludlow & Sherriff 11086* (holotype in Herb. Brit. Mus.).

At first glance this plant might be mistaken for *C. mucronifera* Maxim. but the bracts with their slender petioles are very different from the broadly cuneate or flabellate bracts of that species as illustrated in *Flora Tangutica* t. 24, figs. 19, 20 (1889). There are also other differences. Thus, in the Reting plant (*C. fimbripetala*) the spur is longer and narrower and the lamina of the anticous petal has a strongly fimbriate margin, with a claw almost as wide as the lamina. These Reting gatherings resemble more closely Maximowicz's illustration (*Flora Tangutica*, t. 24, figs. 13–17) and description (p. 50) of his *C. capnoides* var. *tibetica* Maxim. though the similarity is far from perfect. Here again the spur in the Reting plant is longer and narrower,

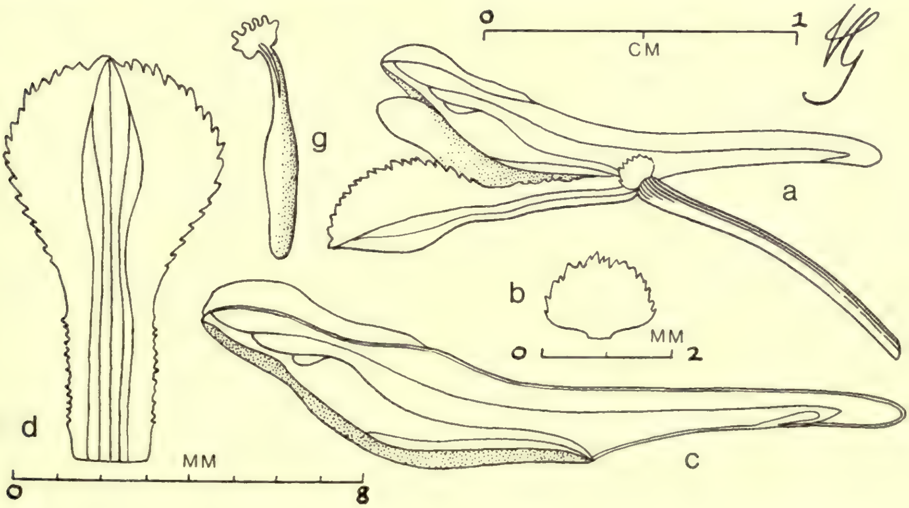


Fig. 4. *Corydalis fimbripetala* Ludlow : a, flower ; b, sepal ; c, posticous petal ; d, anticous petal ; g, gynoecium (*Ludlow & Sherriff 11086*).

and there is nothing in Maximowicz's plant to compare with the frilled margin of the lamina of the lower petal in the Reting plant. Bracts too are different.

Corydalis longibracteata Ludlow, sp. nov. (Plate 6 ; Text-fig. 5)

Species ad sectionem *Rapiferae* Fedde pertinens sed ab omnibus speciebus sectionis floribus 2–4 subumbelliformiter dispositis, bracteis linearibus folii caulini segmentis similibus praecipue distinguenda.

Radices fasciculatae, anguste napiformes, 1–2 cm longae, 2–3 mm latae, fibrosae. *Caulis* gracilis, erectus, haud ramosus, 4–20 cm longus, 1–1·5 mm latus. *Folia radicalia* fugacia, valde minuta, quinquefoliolata, foliolis c. 3·5 mm longis ; petiolo filiformi c. 1–2 cm longo ; *folium caulinum* unum racemo fere contiguum, petiolo 1–2 cm longo, 1 mm lato, lamina ut videtur 5-foliolata segmentis linearibus 1·5–4 cm longis, 1–3 mm latis sed vero trifoliolata foliolo mediano indiviso sed foliolis lateralibus fere ad basin bipartitis. *Inflorescentia* subumbelliformis, 2–4-flora ; pedicelli 8–16 mm longi. *Bracteae* sessiles, inferiores 3–5-segmentatae, ceterae 1–2-segmentatae, segmentis linearibus foliis caulinis similibus. *Flores* horizontales, caerulei vel violaceo-purpurei. *Sepala* minuta squamiformia. *Petalum posticum* c. 17 mm longum (calcari incluso) ecristatum ; calcar 7–8 mm longum, paulum deflexum, obtusum ; lamina late ovata, 9–10 mm longa ; *petalum anticum* c. 10 mm longum, ovatum, basi paulum gibbosum ; *petala interiora* 9 mm longa (ungue 5 mm longo incluso). *Stamina* (*synandria*) c. 5 mm longa, basi dilatata. *Ovarium* oblongo lineare, ovulis c. 20 biseriatis. *Stigma* capitatum bilobatum, lobis ad apicem acutis papillis terminatis. *Capsula* matura ignota, immatura c. 10 mm longa, 2 mm lata.

S.E. TIBET : Kashong La, Chayul Chu (28°20′N, 93°08′E), 4250 m, 'Corolla violet-purple. Open stony scree', 19 July 1936, *Ludlow & Sherriff 2394*. Lusha Chu,

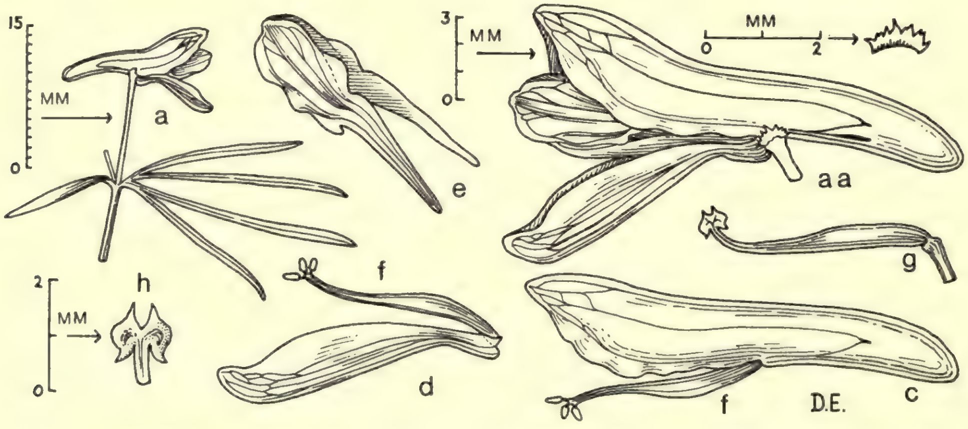


FIG. 5. *Corydalis longibracteata* Ludlow : a, flower with bract. ; aa, flower and sepal ; c, posticous petal ; d, anticous petal ; e, inner petals ; f, phalange with anthers ; g, gynoecium ; h, stigma (*Ludlow, Sherriff & Elliot 15199*).

(29°27′N, 94°35′E), 3500 m, 'In damp grassy sward near river. Perianth segments sky blue, inner segments white at base, tipped purple', 8 June 1938, *Ludlow, Sherriff & Taylor 4698*. Lusha La, south side (29°18′N, 94°37′E), 3800 m, 'Equals 4698 north side of Lusha La', 13 June 1938, *Ludlow, Sherriff & Taylor 4698A*. Deyang La (29°22′N, 94°52′E), 'Bluish purple and white flower on rocks', 3500 m, 8 June 1947, *Ludlow, Sherriff & Elliot 15199* (holotype in Herb. Brit. Mus.).

With its long linear bracts, its small inflorescence of 2–4 flowers and its solitary cauline leaf the present species is not unlike *C. pseudojuncea*, a new species from Nepal. In the Nepal plant, however, the inflorescence is lax, not congested, the flowers yellow, not blue, and the cauline leaf sessile and unsegmented, not petiolate and segmented. Also in the Nepal plant the radical leaf is strongly developed and equal to the flowering stem in length, not dwarfed and degenerate as in the present species.

Corydalis ludlowii Stearn, sp. nov. (Plate 7 ; Text-fig. 6)

Species *C. benecinctae* W. W. Sm. et *C. hemidicentrae* Hand.-Mazz. persimilis, sed foliis simplicibus et indivisis facile distinguenda.

Rhizoma c. 6 cm longum, 4–7 mm latum, ramosum. *Caulis* pars subterranea 3–4 cm longa, 1–1·5 mm lata, squamis 2–4 amplexicaulibus lanceolatis vel ovatis 5–8 mm longis obsita ; pars supraterranea 1–3 cm longa, folia 4–8 quasi-radicalia et scapos 1–3 emittens. *Folia* simplicia ; lamina indivisa, suborbiculata, basi subcordata, integra, 1·25–4 cm longa, 1–4·25 cm lata, crasse carnosa, utrinque glabra, supra virida infra pallidiora, nervis 5–7 indistinctis parce ramosis ; petiolus 4–8 cm longus, 0·75–1 mm latus, basi vaginatus. *Inflorescentia* 3–6-flora, terminalis, umbelliformis ; pedunculus 10–16 cm longus, 1–1·5 mm latus, petiolo robustior ; pedicelli pergraciles, 10–15 mm longi. *Bracteae* 4–6, obovatae vel oblanceolatae, 5–10 mm longae, 3–8 mm latae, involucrum paene formantes. *Flores* horizontales, pallide caerulei (ardesiaci), fauce albo, 15–24 mm longi (calcari incluso). *Sepala* late triangularia, margine denticulata, 1–1·25 mm longa, scariosa, persistentia. *Petalum posticum* (cum calcari) c. 24 mm longum ; calcar cylindricum, apice rotundatum, c. 13 mm longum, 1·5–2 mm latum, glande nectarifera 8 mm longa ; *petalum anticum* c. 13 mm longum, basi nonnihil saccatum, lamina petali postici longior ; *petala interiora* c. 9 mm longa (unguiculo incluso), lamina 4 mm longa, unguiculo filiformi 5 mm longo. *Stamina* (*synandria*) c. 6 mm longa, basi dilatata. *Ovarium* ellipticum, ovulis 11–13 biseriatis ; *stigma* rectangulare, quadri-tuberculatum. *Capsula* vix matura anguste elliptica, 10 mm longa, 3 mm lata ; *Semina* rotundata, laevia, opaca, 1·5 mm diam.

TIBET : Nambu La, Tongyuk River, Pome (29°59′N, 94°19′E), 3650 m, 11 June 1947, *Ludlow, Sherriff & Elliot 13881* (holotype in Herb. Brit. Mus.).

This remarkable species belongs to the section *Corydalis* (i.e. *Eucorydalis* Fedde) subsection *Benecinctae* Fedde (in Engler & Prantl, *Natürl. PflFam.*, 2. Aufl. 17b : 134 (1936)), in which the flowers are arranged in the form of an umbel, the bracts simulate an involucre and the stigma has four tubercles. Fedde has set out the distinctions

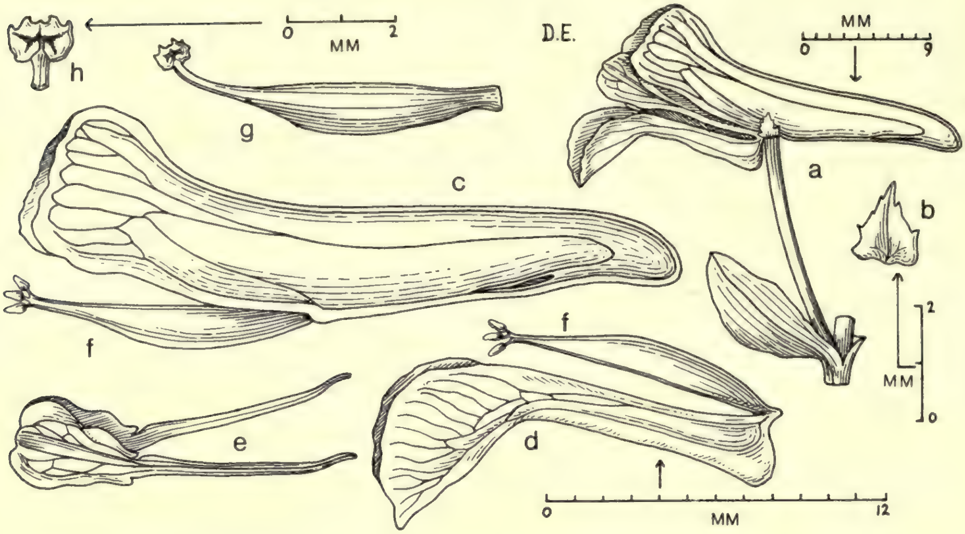


FIG. 6. *Corydalis ludlowii* Stearn : a, flower with bract ; b, sepal ; c, posticous petal ; d, anticous petal ; e, inner petals ; f, phalange with anthers ; g, gynoecium ; h, stigma (*Ludlow, Sherriff & Elliot 13881*).

between the three other species included in this subsection (i.e. *C. benecincta* W. W. Sm., *C. hemidicentra* Hand.-Mazz. and *C. trilobipetala* Hand.-Mazz.) in his *Repertorium Specierum Novarum Regni Vegetabilis* 25 : 222 (1928) ; natives of Yunnan and Szechwan, these have ternately divided leaves and thus differ from the present Tibetan species which has simple undivided leaves, a character unique within the genus. These leaves in size and shape closely resemble those of *Pyrola rotundifolia*. At present the species is known only from the type locality on the Nambu La, where it was quite plentiful in a sandy marsh. Unfortunately, for it is of great interest, no ripe seed was obtained.

W. T. Stearn

Corydalis megacalyx Ludlow, sp. nov. (Plate 8 ; Text-fig. 7)

Species bracteis magnis foliaceis, calyce magno persistente, capsulis valde reflexis notabilis.

Radix elongata, c. 20 cm longa, 3–7 mm crassa, ramosa vel simplex. *Caulis* 2–6 cm longus, squamosus, ramos caespitosos ad 8 cm longos prope vel ad terram edens. *Folia* glauco-grisea. *Folia basalia* 3–6 cm longa (petiolo complanato 1–3 cm longo, 1·5–2 mm lato incluso), ambito anguste ovato, pinnatim 3–4 jugata ; pinna omnis 1–2 paribus pinnularum eis invicem in pinnulis secondariis lobulis ultimis linearibus divisis ; pinnae paris infimi petiolulis bene evolutis c. 6 mm longis, aliae petiolulis gradatim decrescentibus instructae. *Folia caulina* basalibus similia sed minora pinnibus pinnulibusque paucioribus. *Inflorescentia* racemosa, congesta,

7–10-flora ; pedicelli graciles, quam bracteae paulo breviores. *Bracteae* foliaceae, infimae 1·5–2 cm longae, ceterae caulis apicem versus decrescentes, foliis caulinis quoad formam similes sed minores, basi dilatatae plerumque margine denticulato. *Flores* lutei, petalis exterioribus stria atro-brunnea conspicua notatis. *Sepala* persistentia, 2·5–3·5 mm longa, basi 1–2 mm lata, scariosa, margine lacerata. *Petala* posticum 15–17 mm longum (calcari cylindrico recto 7–8·5 mm longo incluso), lamina apiculata, medio brunneo-striata, glande nectarifera c. 4 mm longa ; anticum c. 8·5 mm longum, vitta conspicua mediana 5-venosa atro-brunnea. *Stylus* 2–3 mm longus ; *stigma* reniforme, papillis 8. *Capsula* valde reflexa, elliptica, 4–4·5 mm longa, 2–2·5 mm lata, 4–6-seminalis. *Semina* rotunda, nigra, nitida, c. 1·5 mm diametro.

NEPAL : east of Chalike Pahar (28°40′N, 83°04′E), 4570 m, 'Among sand and rocks on loose screes. Leaves glaucous-grey. Flowers yellow with black centre', 31 July 1954, *Stainton, Sykes & Williams 3697* (holotype in Herb. Brit. Mus.). Muktinath (28°49′N, 83°54′E), 4000 m, 28 July 1954, *Stainton, Sykes & Williams 2050.* Tukucha, Kali Gandaki (28°43′N, 83°39′E), 4250 m, 12 Sept. 1954, *Stainton, Sykes & Williams 7777.* Chalike Pahar, 4400 m, 20 Sept. 1954, *Stainton, Sykes & Williams 4520.* Thakurji Lekh, south of Jumla (29°07′N, 82°14′E), 3650 m, 16 July 1952, *Polunin, Sykes & Williams 4714.* Khangsar (28°40′N, 83°59′E), 4570 m, 27

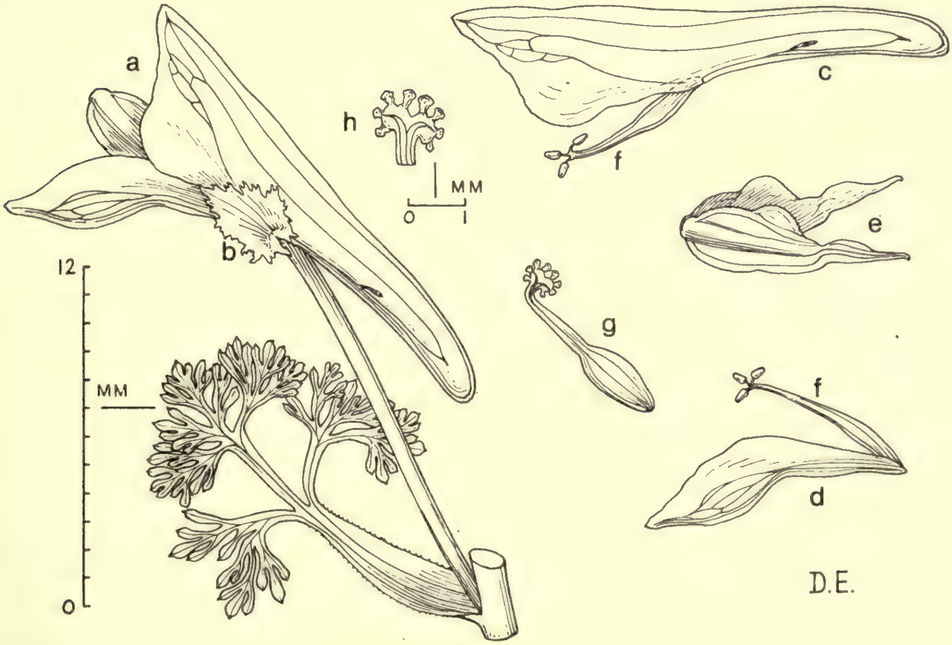


FIG. 7. *Corydalis megacalyx* Ludlow : a, flower with bract ; b, sepal ; c, posticous petal ; d, anticous petal ; e, inner petals ; f, phalange with anthers ; g, gynoecium ; h, stigma (*Stainton, Sykes & Williams 3697*).

July 1950, *Lowndes L1256*. Taglung, south of Tukucha, Kali Gandaki (28°39′N, 83°38′E), 4000 m, 15 July 1954, *Stainton, Sykes & Williams 1796*.

This new species belongs to subsection *Mucroniferae* Fedde. In most species of the genus *Corydalis* the sepals are fugacious and minute, but in the present one they persist and are almost as long as and nearly envelop the ripe capsule. At a casual glance this species is not unlike *C. mucronifera* Maxim. but its finely incised leaves and bracts are very different.

Corydalis oligantha Ludlow, sp. nov. (Plate 9 ; Text-fig. 8)

Caudex brevis, reliquiis paucis basium petiolorum emortuorum coronatus, fibras numerosas filiformes emittens. *Caulis* debilis, gracilis, simplex, 8–12 cm longus, 0·75 mm latus. *Folia basalia* 2–6, caule florifero breviora ; petioli filiformes, usque ad 5 cm longi, 0·5 mm lati ; lamina bipinnatisecta, quoad ambitum late triangularis vel late ovata, 1–1·5 cm longa, 1–2 cm lata, pinnis inferioribus quam superioribus majoribus, omnibus pinnatisectis, segmentis petiolulatis lobulis rotundatis, petiolulis inferioribus 1–1·5 mm longis, superioribus 0·5 mm longis ; pinna terminalis trisecta, lobis obtusis ad medium incisis. *Folium caulinum* solitarium, paulo infra inflorescentiam positum, foliis basalibus simile sed minus, petiolo breviore ; bulbillus axillaris interdum adest. *Inflorescentia* 2–3-flora ; pedicelli erecti graciles, 7–15 mm longi. *Bracteae* foliaceae, infima folio caulino similis sed pinnis paucioribus, aliae parviores. *Flores* albi, malvini vel pallide caerulei. *Sepala* reniformia, margine dentata, 1 mm lata. *Petalum posticum* sine crista ; lamina 8–9 mm longa, 4–5 mm lata ; calcar rectum cylindricum, 8–9 mm longum, glande nectarifera 4 mm longa ;

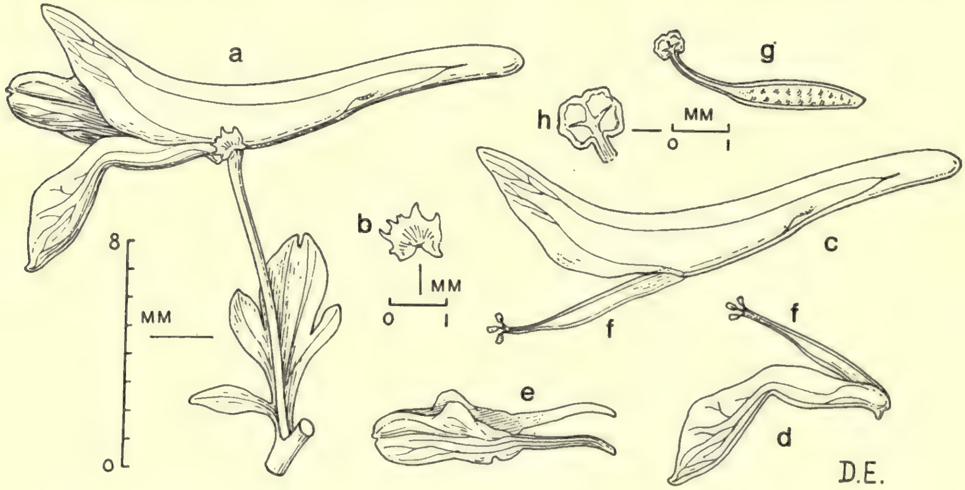


FIG. 8. *Corydalis oligantha* Ludlow : a, flower with bract ; b, sepal ; c, posticous petal ; d, anticous petal ; e, inner petals ; f, phalange with anthers ; g, gynoecium ; h, stigma (*Ludlow, Sherriff & Hicks 20266*).

petalum anticum 8–9 mm longum, basi dentatum; *petala interiora* 7 mm longa, lamina 4 mm longa, ungue 3 mm longo. *Ovarium* lineare vel lineari-oblongum. *Stylus* 1·5 mm longus; *stigma* globosum vel rotundatum, papillis anterioribus 4. *Capsula* immatura c. 8 mm longa, 1·5 mm lata.

BHUTAN: Sergong La, Kuri Chu Valley (27°52′N, 91°03′E), 3050 m, 'flowers pale blue, on banks in fir and rhododendron forest', 9 May 1949, *Ludlow, Sherriff & Hicks 18848.* Lao, Lao Chu (27°52′N, 91°28′E), 2900 m, 'flowers white, moist soil in clearings', 12 May 1949, *Ludlow, Sherriff & Hicks 20266* (holotype in Herb. Brit. Mus.).

ASSAM: Manda La, Balipara Frontier Tract (27°15′N, 92°15′E), 3000–3500 m, 'flowers mauve on damp shady banks in Conifer–Rhododendron forest', 19 May 1935, *Kingdon Ward 11470.*

This little woodland plant grows in moss in the rhododendron and conifer forests of eastern Bhutan and the adjoining Balipara Frontier Tract of Assam, nowadays known as the North East Frontier Agency. Of the 60 plants available none exceeds 12 cm in height. The inflorescence normally consists of two flowers only; very occasionally there are three, but never more, hence the specific epithet. The closest ally of this new species would appear to be *C. stenantha* Franch.

Corydalis oxalidifolia Ludlow, sp. nov. (Plate 10; Text-fig. 9)

Species ex affinitate *Corydalis jigmei* C. E. C. Fischer & Kaul a qua foliis ternatis, non biternatis, inter alia differt.

Rhizoma brevissimum, radicibus fasciculatis napiformibus incrassatis 12–16 mm longis et 1–3 mm crassis, ad apicem squamis ovatis carnosis c. 7–10 mm longis et 3–5 mm latis vestitum, e quarum axillis caules floriferi 2–4 et folia basalia 2–4 longitudine eos aequantia oriuntur. *Folia basalia* 4–6 cm longa, lamina ternata, foliolis erectis 6–8 mm longis, 3–4 mm latis, segmentis lateralibus in partibus duobus fere ad basin divisis, segmento medio integro obovato vel interdum bilobato; petiolus 3–5 cm longus, 0·5–0·75 mm latus, vaginatus; petioluli 1 mm longi. *Folia caulina* nulla. *Caulis* 4–6 cm longus, 0·75 mm crassus, erectus, aphyllus. *Inflorescentia* congesta, 2–4-flora; pedicelli 3–4 mm longi. *Bracteae* 2 vel 4, foliaceae, sessiles, infima c. 8 mm longa et lata in segmentis 3–5 divisa, summa saepe indivisa vel interdum leviter lobata. *Flores* parvi, horizontales, caerulei, faucibus albis, bracteis semi-occultis. *Sepala* minuta, 0·75 mm longa, manifeste fugacia. *Petalum* posticum (calcari incluso) 8–10 mm longum, subacutum, ecristatum, lamina 5–6·5 mm longa, calcari cylindrico 3–3·5 mm longo 1·5 mm lato obtuso; petalum anticum 6·5 mm longum, subacutum. *Ovarium* (immaturum) anguste ellipticum c. 3 mm longum, ovulis biseriatis. *Stylus* 1·5–2 mm longus; stigma capitatum. *Capsula* (immatura) anguste elliptica, 6 mm longa, 2 mm lata.

BHUTAN: Me La (27°55′N, 91°33′E), 4250 m, 4 Aug. 1933, *Ludlow & Sherriff 372.* Shingbe (Me La), 4570 m, 29 June 1949, *Ludlow, Sherriff & Hicks 20422* (holotype in Herb. Brit. Mus.).

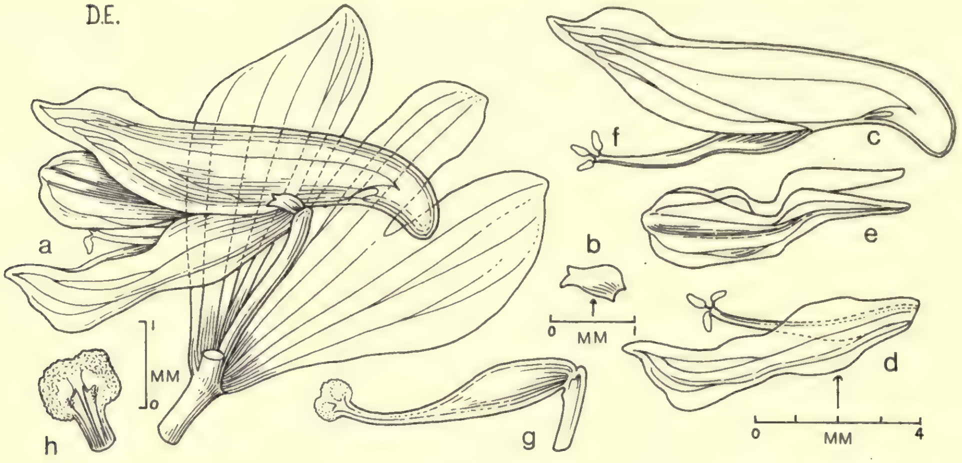


FIG. 9. *Corydalis oxalidifolia* Ludlow: a, flower with bract; b, sepal; c, posticous petal; d, anticous petal; e, inner petals; f, phalange with anthers; g, gynoecium; h, stigma (*Ludlow, Sherriff & Hicks 20422*).

Somewhat similar in appearance to *C. jigmei* C. E. C. Fischer & Kaul, this species is distinguished by its ternate not biternate leaves which are broadly, not narrowly, segmented. The flowers, 2–4 in number, are almost hidden by the large foliaceous bracts and do not protrude as in *C. jigmei*. Moreover there is no cauline leaf.

Corydalis pseudojuncea Ludlow, sp. nov. (Plate 11; Text-fig. 10)

C. juncea affinis, a qua, inter alia, bracteis linearibus multo longioribus, racemis laxis 2–6-floris, petalis interioribus apice non purpureis, calcari laminam aequante differt.

Radices 2–4, parvae, 10–20 mm longae, 3–6 mm crassae, fasciculatae, tenuiter fibrosae. *Caulis* erectus, gracilis, 15–35 cm longus, 1 mm latus, attenuatus. *Folia basalia* caules aequantia; petiolus pergracilis, ad 26 cm longus, 0·5 mm latus, apice trifoliolatus; foliola omnia tripartita; foliolorum segmenta acuta, linearia, trinervia, 2·5–5 cm longa, 2–3 mm lata; petiolulus segmenti medii 7 mm longus, segmentorum lateralium 2 mm longus. *Folium caulinum* unum sessile, lineare, 3–4 cm longum, 2 mm latum. *Inflorescentia* racemosa, laxa, 2–6-flora; pedicelli 4–8 mm longi. *Bracteae* sessiles, lineares, 2·5–4 cm longae, 1–2 mm latae, folio caulino persimiles. *Flores* horizontales, lutei; pedicelli 4–8 mm longi. *Sepala* minuta, ut videtur mox caduca. *Petalum* posticum c. 16 mm longum (calcari incluso); calcar rectum, anguste cylindricum, subacutum, c. 8 mm longum, 1 mm latum; lamina 8 mm longa, glande nectarifera 5 mm longa; petalum anticum 7–8 mm longum, basi parum gibbosum; petala interiora pallide lutea apice haud purpurea. *Ovarium* immaturum lineare, c. 4 mm longum, 0·5 mm latum. *Stylus* 2·5 mm longus; stigma semilunaris, papillis 4. *Capsula* ignota.

NEPAL: Margor Lagna (29°53′N, 81°57′E), 3960 m, 16 June 1952, *Polunin, Sykes & Williams 4319*. Near Jangla Bhanjyang (28°51′N, 82°56′E), 3960 m, 'Gentle grassy slopes, usually found right among tufts of grass or other plants. Especially fond of small grassy gullies. Flowers lemon yellow', 2 July 1952, *Polunin, Sykes & Williams 2360* (holotype in Herb. Brit. Mus.). Bhurchula Lekh near Jumla (29°14′N, 82°07′E), 3810 m, 14 July 1952, *Polunin, Sykes & Williams 4688*. Maharigaon (29°22′N, 82°24′E), 4420 m, 13 July 1952, *Polunin, Sykes & Williams 136*. Sisne Himal, 4250 m, 17 June 1966, *Shrestha 5128*.

Corydalis pseudojuncea resembles *C. juncea Wall.* but differs in many particulars. Its spur is tapering, subacute and as long as or sometimes even longer than the narrow lamina, whereas in the Wallichian plant the spur is blunt and a good deal shorter than the lamina. The two inner petals of *C. juncea* have conspicuous purple tips which are lacking in this new species. Although the bracts in *C. juncea* vary considerably they are never so consistently elongated as in *C. pseudojuncea*, where they are many times longer than the pedicels and even much longer than the flowers. The inflorescence is lax, with the flowers few, never more than six, and normally only two or three. The foliage and bracts are very similar to those in *C. crithmifolia* Royle, but the root system is quite different, and Royle's plant has no cauline leaf.

On the type-sheet of *C. pseudojuncea* (Pl. 11) there is also mounted a specimen (the sixth from the right) of *C. juncea*, easily distinguished from the others by its very

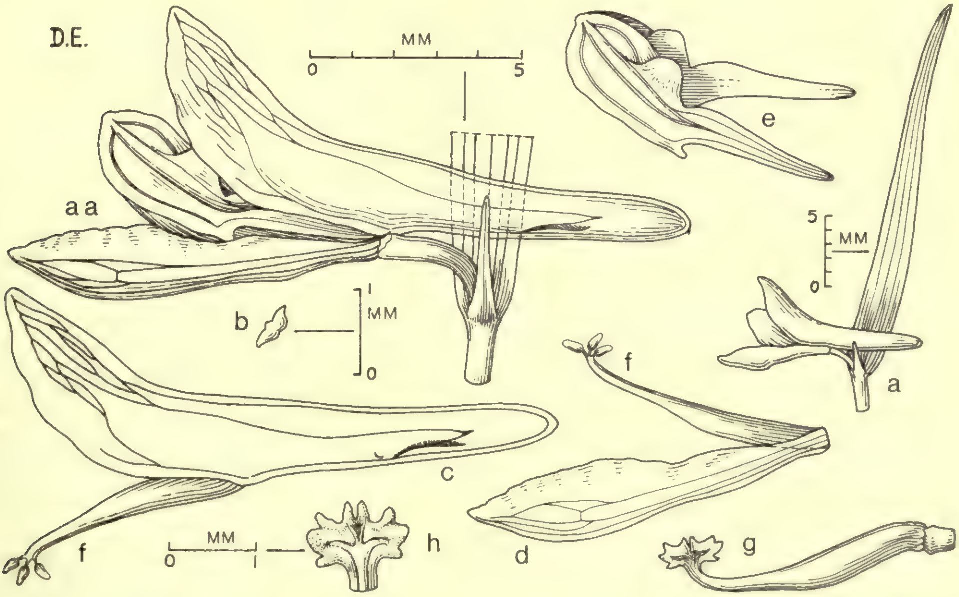


FIG. 10. *Corydalis pseudojuncea* Ludlow: a, flower with bract; aa, flower; b, sepal; c, posticous petal; d, anticous petal; e, inner petals; f, phalange with anthers; g, gynoecium; h, stigma (*Polunin, Sykes & Williams 2360*).

short bracts. That the two species grow in the same habitat but keep distinct is evident from *Polunin, Sykes & Williams 136*, which is likewise a mixed gathering.

The spur of the posticous petal in *C. pseudojuncea* is usually more slender than is portrayed in Text-fig. 10.

Corydalis quinquefoliolata Ludlow, sp. nov. (Plate 12 ; Text-fig. 11)

Herba perennis, glabra, ad 40 cm alta. *Radices* fasciculatae, tuberosae, 3–4 cm longae, 2·5 mm crassae, fibras filiformes emittentes. *Caules* 1–3, erecti, ad 40 cm longi, simplices vel saepe ramos axillares 1–2 efferentes. *Folia basalia* 2–4, erecta, imparipinnata, 15–25 cm longa (petiolo 5–18 cm longo incluso) ; foliola 5, alterna, petiolulata, lanceolata vel anguste oblonga, basi anguste cuneata, apice acuta, 3–5 cm longa, 0·7–1 cm lata, nervis subparallelis 5–8 percursa ; *folia caulina* interdum nulla sed plerumque basalibus similia foliolis jugatim dispositis. *Inflorescentia* racemosa, primo congesta, demum laxior, 6–12-flora ; pedicelli 2–12 mm longi. *Bracteae* integrae, lanceolatae, 1 cm longae. *Flores* aurei. *Sepala* minutissima. *Petalum posticum* 13·5 mm longum (calcari incluso) ; cristatum ; calcar validum curvatum, 6·5 mm longum, glande nectarifera gracile c. 3·5 mm longa ; *petalum anticum* 9 mm longum ; *petala interiora* 8 mm longa (ungue 4 mm longo incluso). *Ovarium* immaturum ellipticum, c. 5 mm longum, 2 mm latum ; *stylus* gracilis,

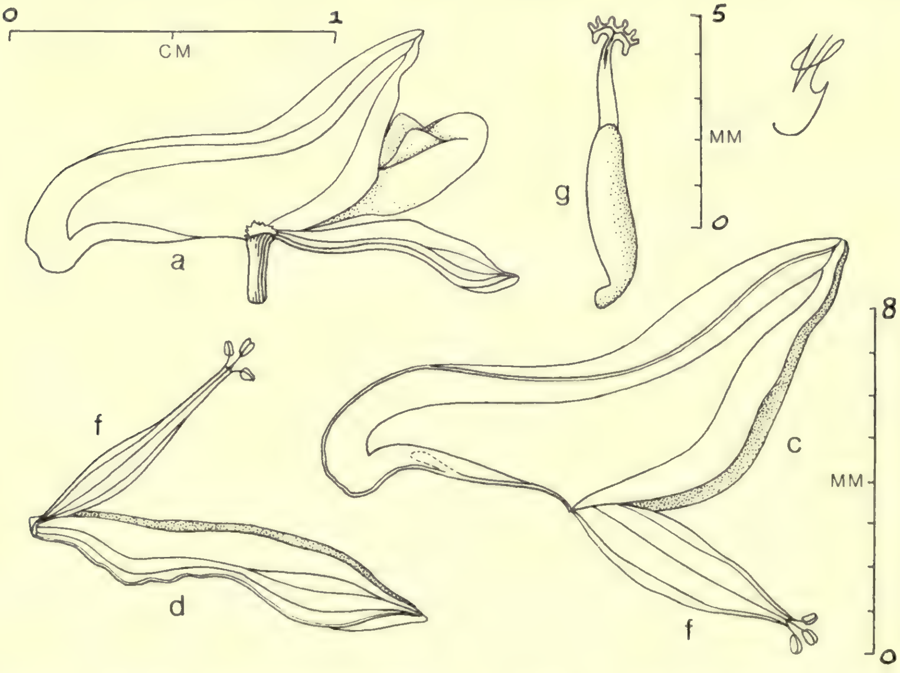


FIG. 11. *Corydalis quinquefoliolata* Ludlow : a, flower ; c, posticous petal ; d, anticous petal ; f, phalange with anthers ; g, gynoecium (*Ludlow, Sherriff & Taylor 5503*).

2 mm longus ; *stigma* c. 2 mm longum, 0·7 mm latum, papillis anterioribus 4, lateralibus 2, cornubus posterioribus 2.

TIBET : Langong (28°45′N, 94°00′E), 3600 m, 'Flowers golden yellow. 1–1½ ft high. Growing on edge of shrub forest in wet ground', 9 June 1938, *Ludlow, Sherriff & Taylor 5503* (holotype in Herb. Brit. Mus.).

The nearest relative of this new species would appear to be *Corydalis delavayi* Franchet, from which it can be immediately distinguished by its quinquefoliolate radical and cauline leaves.

Corydalis staintonii Ludlow, sp. nov. (Plate 13 ; Text-fig. 12)

Herba caespitosa c. 20 cm alta et in speciminibus bene evolutis 30 cm diametro. *Caudex* c. 2 cm diametro reliquiis lignosis persistentibus basium petiolorum cauliumque emortuorum dense coronatus. *Caules* floriferi numerosi, simplices, usque ad 20 cm alti. *Folia* numerosa, omnia basalia, usque ad 18 cm longa (petiolo gracili basi vaginato 7–8 cm longo incluso) ; lamina pinnata ; pinnae alternae, 5–6 utrinque, c. 1·5 cm longae, inferiores bi- vel tri- vel quadri-lobulatae, infima brevissime petiolulata, superae lanceolatae vel late lanceolatae, integrae, sessiles, terminalis triloba. *Folium caulinum* nullum, sed bractea infima interdum flore caret et folium caulinum simulat. *Inflorescentia* racemosa, laxa, 12–18-flora, 5–7 cm longa ; pedicelli graciles 3–5 cm longi. *Bracteae* magnae conspicuae, infima 3·5 cm

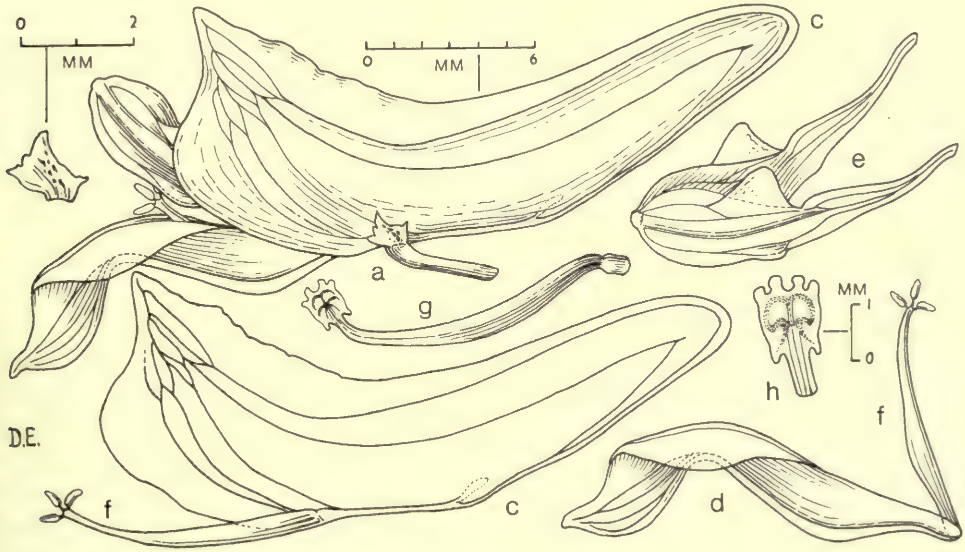


FIG. 12. *Corydalis staintonii* Ludlow : a, flower ; b (top left fig.), sepal ; c, posticous petal ; d, anticous petal ; e, inner petals ; f, phalange with anthers ; g, gynoecium ; h, stigma (*Stainton 5484*).

longa, 2–3-pinnatisecta, lobata, lobis lanceolatis subobtusis, 15 mm longis, 3 mm latis, medianae et superae quadri- vel tri-lobatae, gradatim decrescentes. *Flores* magni, lutei, semi-lunares. *Sepala* minuta, scariosa, 1 mm longa. *Petalum* posticum semi-lunaris, cristatum, usque ad 29 mm longum (calcari crasso 14–15 mm longo, apice 3 mm lato, ad insertionem pedicelli 5 mm lato, incluso), glande nectarifera 7 mm longa longitudine ½ calcaris attingente ; petalum anticum 14–15 mm longum, cristatum, haud gibbosum sed denticulo basi munitum ; petala interiora 12 mm longa (ungue gracili 6 mm longo incluso). *Phalanges* 10 mm longae. *Ovarium* lineare ; *stylus* 2–3 mm longus ; *stigma* subglobosum, 1 mm diametro, papillis anterioribus 4, cornibus posterioribus 2. *Capsula* immatura 20 mm longa, 2 mm lata. *Semina* biseriata, 20–25, impolita, leviter striata, carunculata.

NEPAL : Toridwari, Bhanjyang (28°50′N, 82°42′E), 3800 m, 'On wet rocks, leaves glaucous, flowers bright yellow', 3 July 1966, *Stainton 5484* (holotype in Herb. Brit. Mus.). Toridwari, 4115 m, 4 July 1966, *Shrestha 5298*.

This is a plant of great beauty. In a genus renowned for the gracefulness and charm of its flowers and foliage it can nevertheless have but few rivals. More than 100 flowers, each 2·5 cm or more in length, were borne on the dozen stems forming the clump of the type specimen. The plant is apparently rare, for, though Nepal has been well worked of recent years, it has, so far, been found only in this one locality. Its nearest relative would appear to be *Corydalis sykesii* Ludlow, another chasmophyte discovered during the Stainton, Sykes & Williams Expedition of 1954, which differs in having straight not semi-lunar flowers and radical leaves with opposite or subopposite trifid pinnae. It commemorates Mr John D. Adam Stainton, its discoverer and the author of *Forests of Nepal* (1972).

Corydalis sykesii Ludlow, sp. nov. (Plate 14 ; Text-fig. 13)

Herba perennis, caespitosa, glabra. *Radix* validus 1 cm crassus, apice reliquiis lignosis caulium petiolorumque dense vestita. *Caules* 6–9 cm alti, numerosi, simplices. *Folia* omnia basalia, 5–8 cm longa (petiolo gracile 3–5 cm longo incluso) ; lamina pinnata, pinnis utroque latere rhachidis tenuissimae 2–3 oppositis, suboppositis vel alternis, infimis breviter petiolulatis mediis subsessilibus summis sessilibus, omnibus regulariter bi- vel tri-lobatis, lobis obovatis, obtusis. *Inflorescentia* racemosa, 3–8-flora ; pedicelli ad 4 cm longi. *Bracteae* infimae 20–30 mm longae, dimidio proximali integro cuneato 8–12 mm longo, 2–3 mm lato, dimidio distali pinnatipartito segmentis oblanceolatis obtusis, 5–8 mm longis, ceterae sursum decrescentes, dimidio proximali integro cuneato dimidio distali trilobato. *Flores* lutei. *Sepala* minuta, dentata, 0·75 mm diam. *Petalum posticum* c. 24 mm longum (calcari incluso), cristatum ; calcar rectum, 13–14 mm longum, glande nectarifera 7 mm longa ; *petalum anticum* 13 mm longum, cristatum ; *petala interiora* 11 mm longa (ungue 5 mm longo incluso). *Ovarium* immaturum anguste ellipticum, 5 mm longum ; *stylus* gracilis ; *stigma* orbiculatum ad late rectangulare, indistincte papillatum. *Capsula* immatura anguste elliptica.

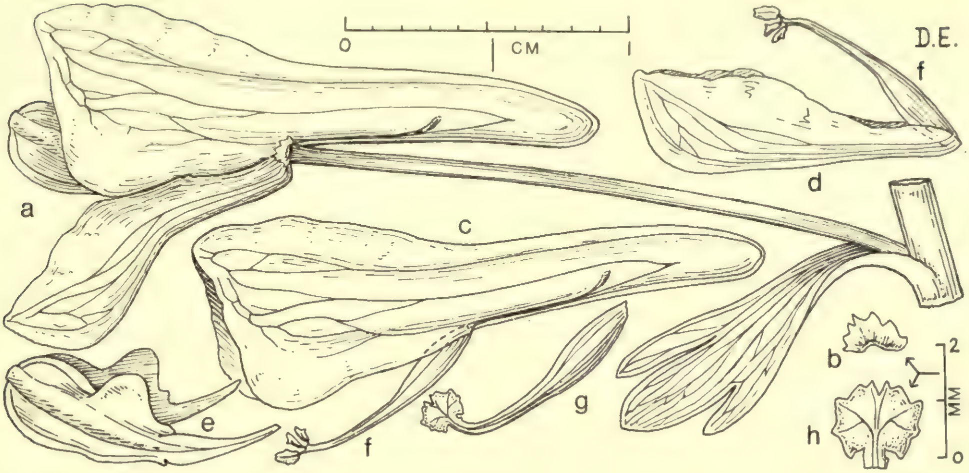


FIG. 13. *Corydalis sykesii* Ludlow : a, flower with bract ; b, sepal ; c, posticous petal ; d, anticous petal ; e, inner petals ; f, phalange with anthers ; g, gynoecium ; h, stigma (*Stainton, Sykes & Williams 2999*).

NEPAL : Above Sauwala Khola (28°39′N, 83°12′E), 4250 m, 'Among rock boulders. Flowers yellow with blackish anthers', 5 June 1954, *Stainton, Sykes & Williams 2999* (holotype in Herb. Brit. Mus.).

This new species is very closely allied to *Corydalis chasmophila* Ludlow but may be distinguished by the structure of its leaves and bracts. In the present species all the pinnae of the leaves are regularly and uniformly bi- or tri-lobed, whereas in *C. chasmophila* the pinnae are pinnatisectly or palmatisectly divided. The bracts, though similar in number and in their overall plan, differ greatly in appearance. In general, the expanded basal half of the bracts is much longer and wider and the lobing of the distal half coarser and more obtuse in *C. sykesii* than it is in *C. chasmophila*, where the expanded base of the bracts is very small and their lobing narrower and more acute. The flowers of *C. sykesii* are appreciably larger than those in *C. chasmophila* ; otherwise they differ very little in floral structure. This species is named in honour of one of its collectors, William Russell Sykes (see *Bull. Br. Mus. nat. Hist.* (Bot.) *2* : 367 (1962)), now on the botanical staff of the Department of Scientific and Industrial Research, Christchurch, New Zealand.

Corydalis tsariensis Ludlow, sp. nov. (Plate 15 ; Text-fig. 14)

Species *C. polyphyllam* Hand.-Mazz. simulans sed floribus flavis (nec caeruleis nec violaceis) et calcari petali postici lamina longiore vel laminam aequante (nec multo breviore) distincta.

Herba perennis, glabra, c. 8 cm alta. *Radix* ramosa vel simplex, ad 20 cm longa, 0·5 cm crassa, apice reliquiis marcidis caulium petiolorumque coronata. *Caules* 2–4, folia basalia aequantes vel his paulo breviores, nudi usque ad bracteam infimam

florem longipedicellatum vel ramulum parvum 2–3 florum subtendentem. *Folia* omnia basalia, numerosa, ad 9 cm longa (petiolo 4–5 cm longo basi vaginato incluso); lamina ambitu ovato-lanceolata, bipinnata, 3–4-jugata, pinnis sursum decrescentibus, infimis petiolulatis 1–1·5 cm longis, superis subsessilibus vel sessilibus, pinnulorum segmentis multisectis, lobis numerosis linearibus acutis c. 0·2 mm latis. *Inflorescentia* racemosa, primo congesta, demum laxior, 6–12-flora; pedicelli ad 2·5 cm longi. *Bracteae* foliaceae, infima pinnata, foliis basalibus similis sed minor, 1–2 cm longa, ceterae sursum decrescentes, supernae flabellatae. *Flores* flavi (sulphurei). *Sepala* semi-orbicularia, 1·5 mm diam., lacerata vel valde dentata, decidua. *Petalum posticum* 19–20 mm longum (calcari incluso), cristatum; calcar cylindricum 9–10 mm longum, glande nectarifera 5·5 mm longa; *petalum anticum* c. 11 mm longum, cristatum. *Ovarium* ellipticum; stigma rectangulare, papillis 4. *Capsula* non visa.

TIBET: Lapu, Tsari (28°42′N, 93°22′E), 4500 m, 'flowers sulphur yellow, . . . on very wet stony river banks', 17 June 1936, *Ludlow & Sherriff 2166* (holotype in Herb. Brit. Mus.). Tso Ga, Tsari (28°40′N, 93°42′E), 4250 m, 'flowers yellow. A scree plant growing with Eriophyton scattered on slate mud screes', 8 July 1935, *Kingdon Ward 11938*. Sobhe La, Pome (30°07′N, 94°54′E), 4250 m, 2 August 1935, *Kingdon Ward 12118*.

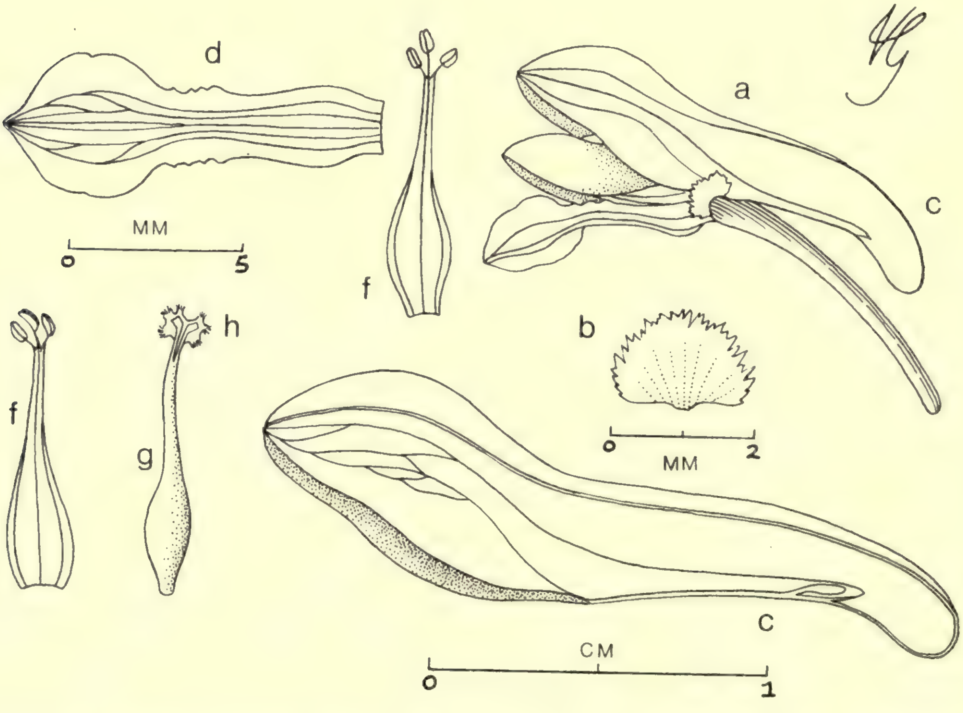


FIG. 14. *Corydalis tsariensis* Ludlow: a, flower; b, sepal; c, posticous petal; d, anticous petal; f, phalange with anthers; g, gynoecium (*Ludlow & Sherriff 2166*).

This plant bears some resemblance to *Corydalis polyphylla* Hand.-Mazz. but the latter has blue or violet flowers with the spur of the posticous petal shorter than the lamina, and not equal to, or longer than, the lamina as in *C. tsariensis*, which has yellow flowers. There is also some similarity, especially as regards foliage and root system, to *C. meifolia* var. *cornutior* Marq. & Shaw, but the flowers of the latter are very much smaller, i.e. 14–15 mm long, including a spur of 5–6 mm, compared with a flower 19 mm long, with a spur of 9 mm in *C. tsariensis*. The bracts too are very different.

F. LUDLOW, O.B.E., M.A.
(deceased 1972)
WILLIAM T. STEARN, D.SC., SC.D., FIL. DR.
Department of Botany
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON SW7 5BD

PLATE 1

Corydalis alburyi Ludlow (*Stainton 5571* ; holotype)

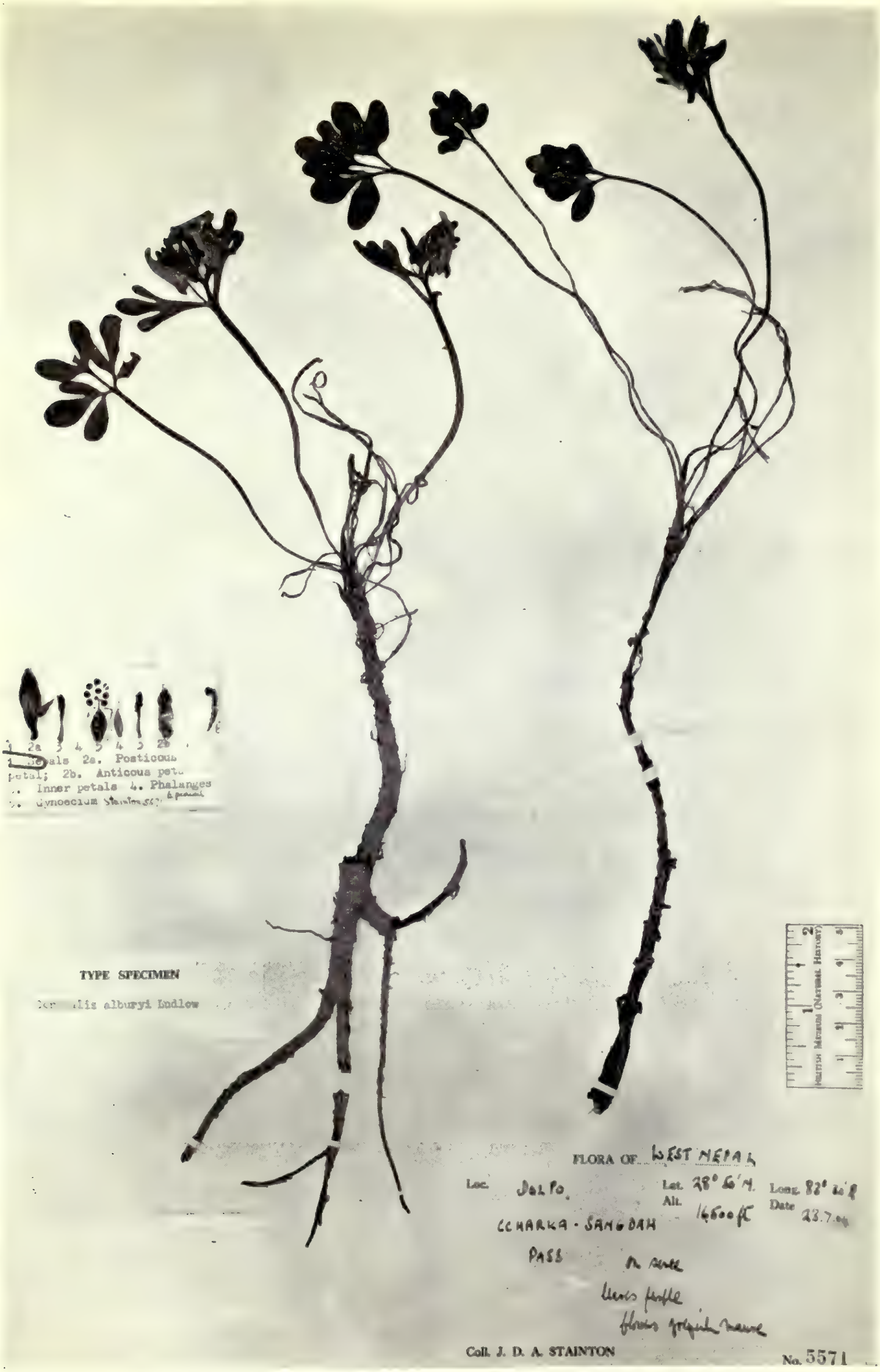

1 2a 3 4 5 4 3 2b
1. Sepals 2a. Posticous
petal; 2b. Anticous pet.
3. Inner petals 4. Phalanges
5. Gynoecium Stainton 5571
TYPE SPECIMEN
Cor lis alburyi Ludlow
FLORA OF WEST NEPAL
Loc. Dolpo.
Lat. 28° 56' N.
Long. 82° 26' E
Alt. 16500 ft
Date 23.7.64
CCHARKA - SANGDAH
PASS
on scree
Leaves purple
flowers yellowish mauve
Coll. J. D. A. STAINTON
No. 5571
BRITISH MUSEUM (NATURAL HISTORY)

PLATE 2

Corydalis aurantiaca Ludlow (*Ludlow, Sherriff & Hicks 16830* ; holotype)

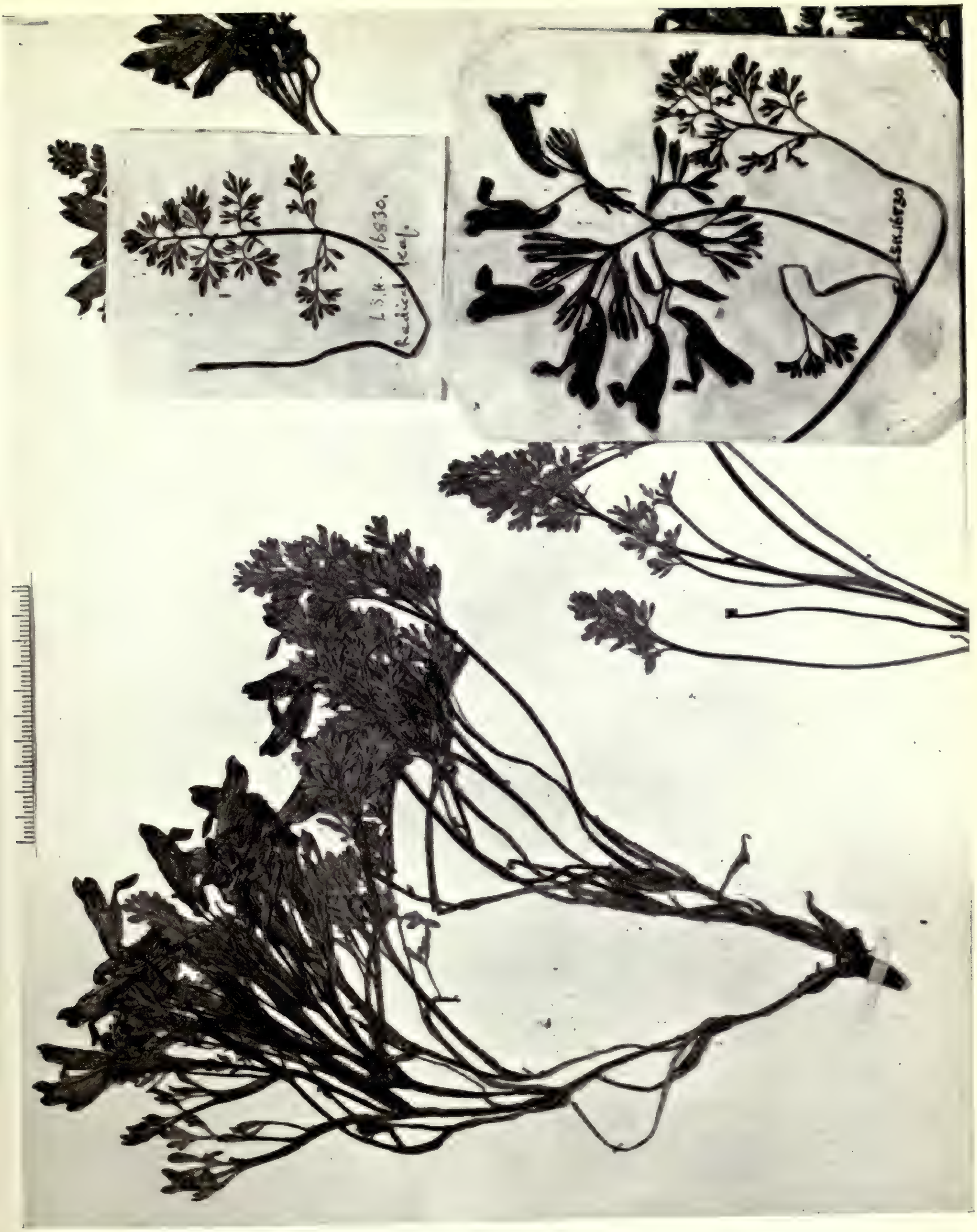
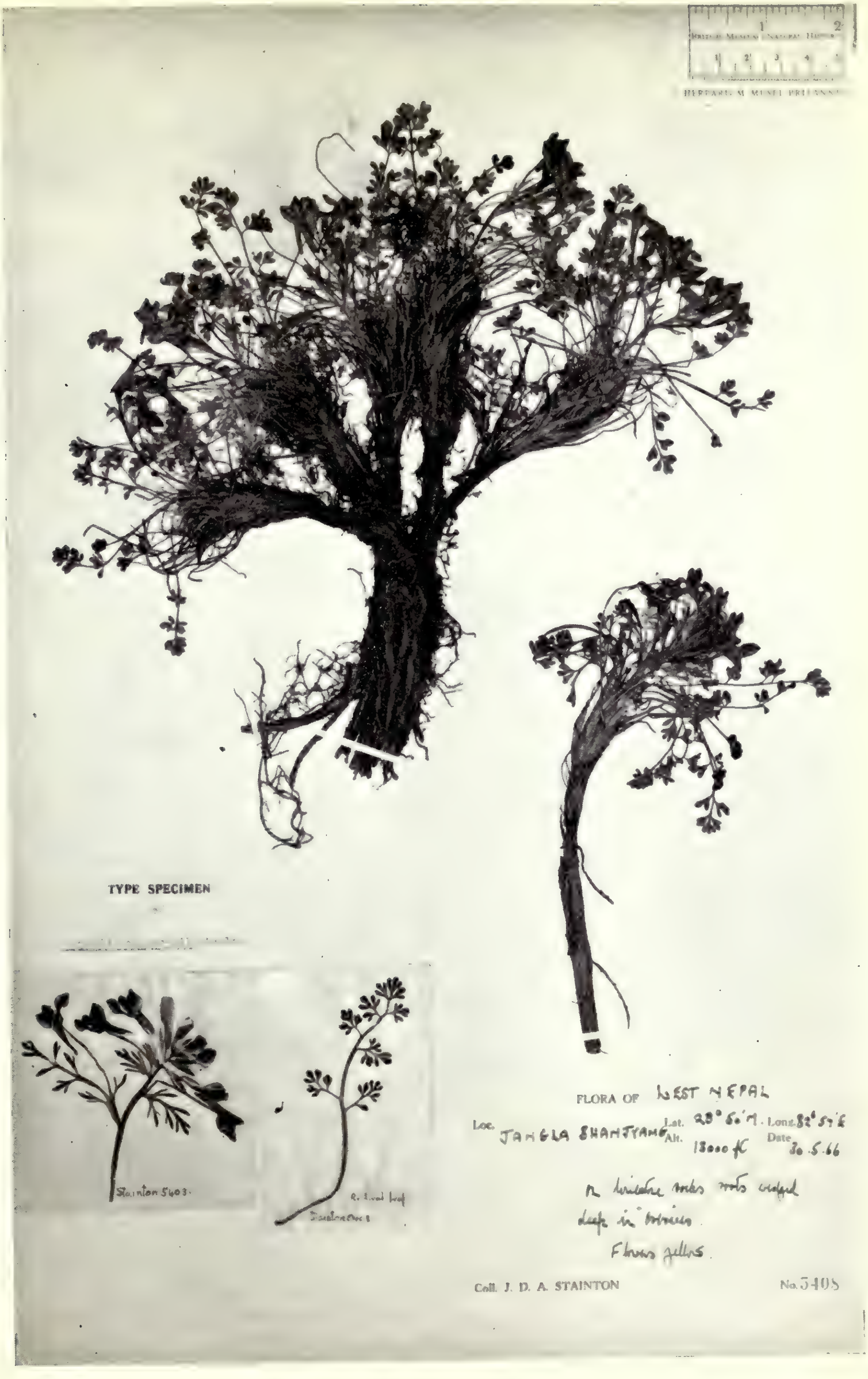

L.S.K. 16830.
Radical leaf.
LSK.16830

PLATE 3

Corydalis chasmophila Ludlow (*Stainton 5408* ; holotype)


BRITISH MUSEUM (NATURAL HISTORY)
HERBARIUM MUSEI BRITANNICI
TYPE SPECIMEN
Stainton 5403.

FLORA OF WEST NEPAL

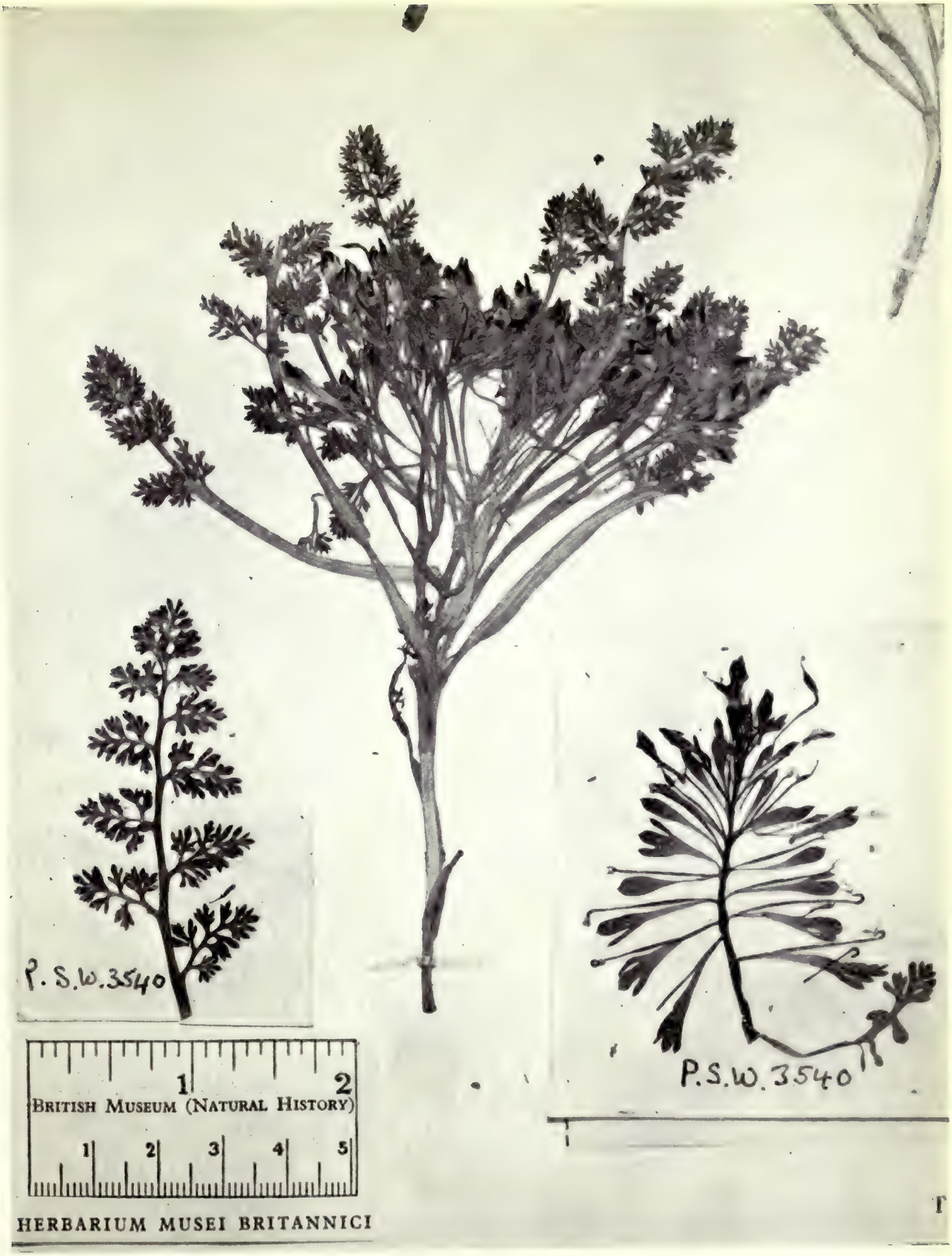
Loc. JANGLA BHANJYANG Lat. 28° 50' N. Long. 82° 57' E
Alt. 13000 ft Date 30.5.66

In limestone rocks roots wedged deep in crevices.
Flowers yellow.

Coll. J. D. A. STAINTON No. 5408

PLATE 4

Corydalis clavibracteata Ludlow (*Polunin, Sykes & Williams 3540* ; holotype)


P.S.W. 3540
P.S.W. 3540
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BRITISH MUSEUM (NATURAL HISTORY)
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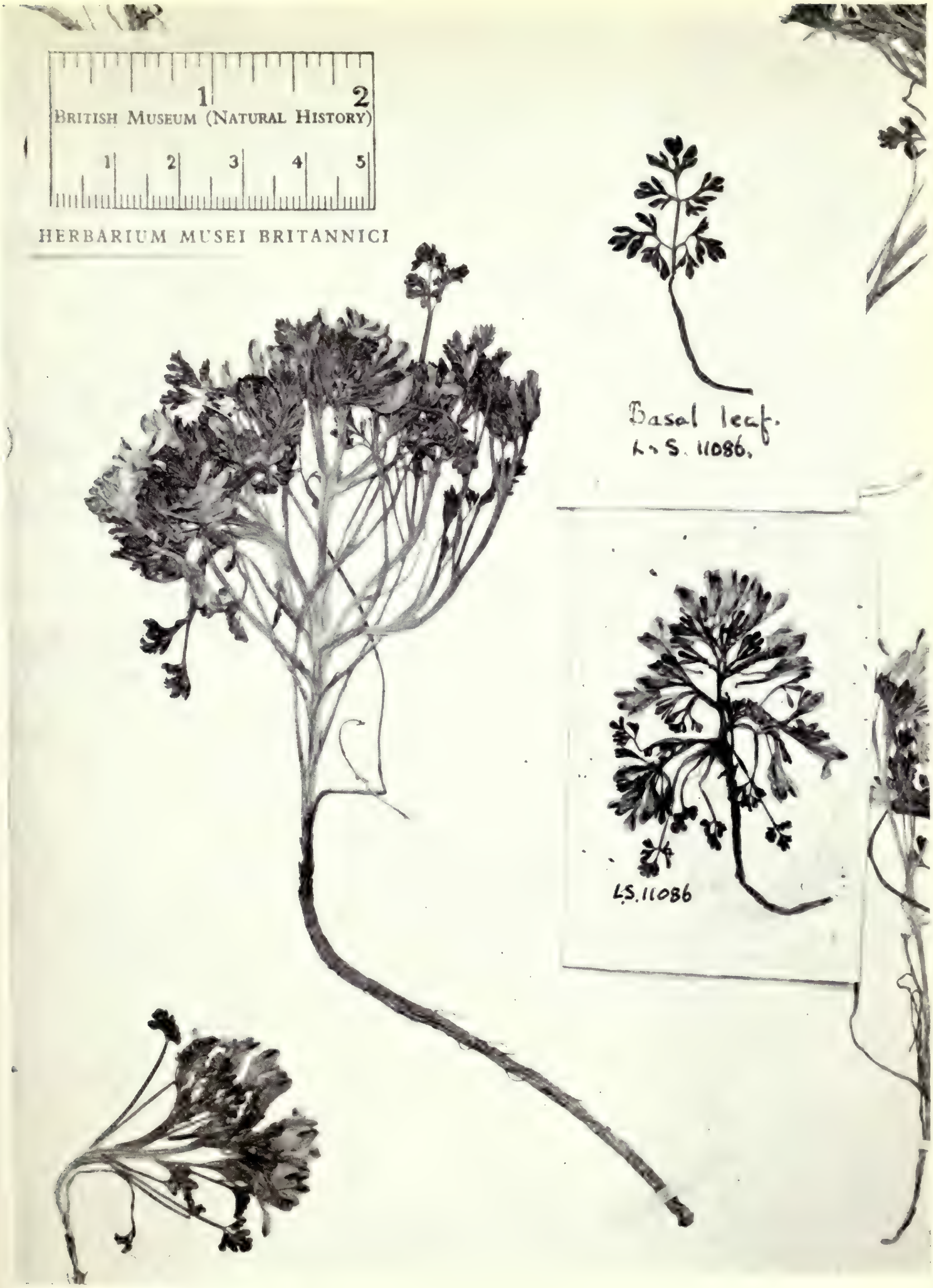
HERBARIUM MUSEI BRITANNICI

PLATE 5

Corydalis fimbripetala Ludlow (*Ludlow & Sherriff 11086* ; holotype)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BRITISH MUSEUM (NATURAL HISTORY)
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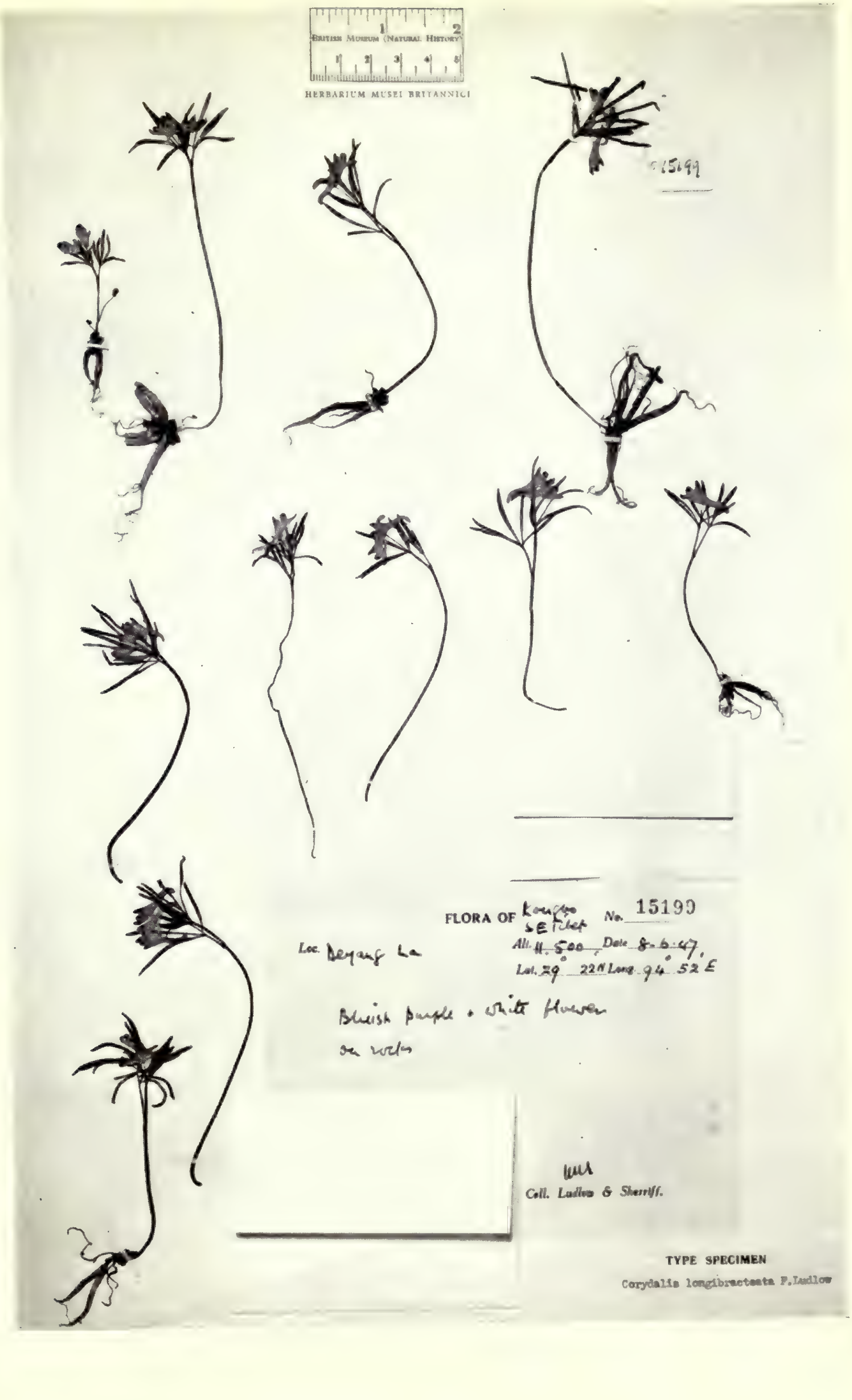
HERBARIUM MUSEI BRITANNICI
Basal leaf.
L. S. 11086.
L.S. 11086

PLATE 6

Corydalis longibracteata Ludlow (*Ludlow, Sherriff & Elliot 15199* ; holotype)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BRITISH MUSEUM (NATURAL HISTORY)
1 2 3 4 5
HERBARIUM MUSEI BRITANNICI
15199

FLORA OF Kongbo SE Tibet No. 15199

Loc. Deyang La

Alt. 11,500 Date 8.6.47.

Lat. 29° 22 N Long. 94° 52 E

Bluish purple & white flowers on rocks

Coll. Ludlow & Sherriff.

TYPE SPECIMEN

Corydalis longibracteata F.Ludlow

PLATE 7

Corydalis ludlowii Stearn (*Ludlow, Sherriff & Elliot 13881* ; holotype)

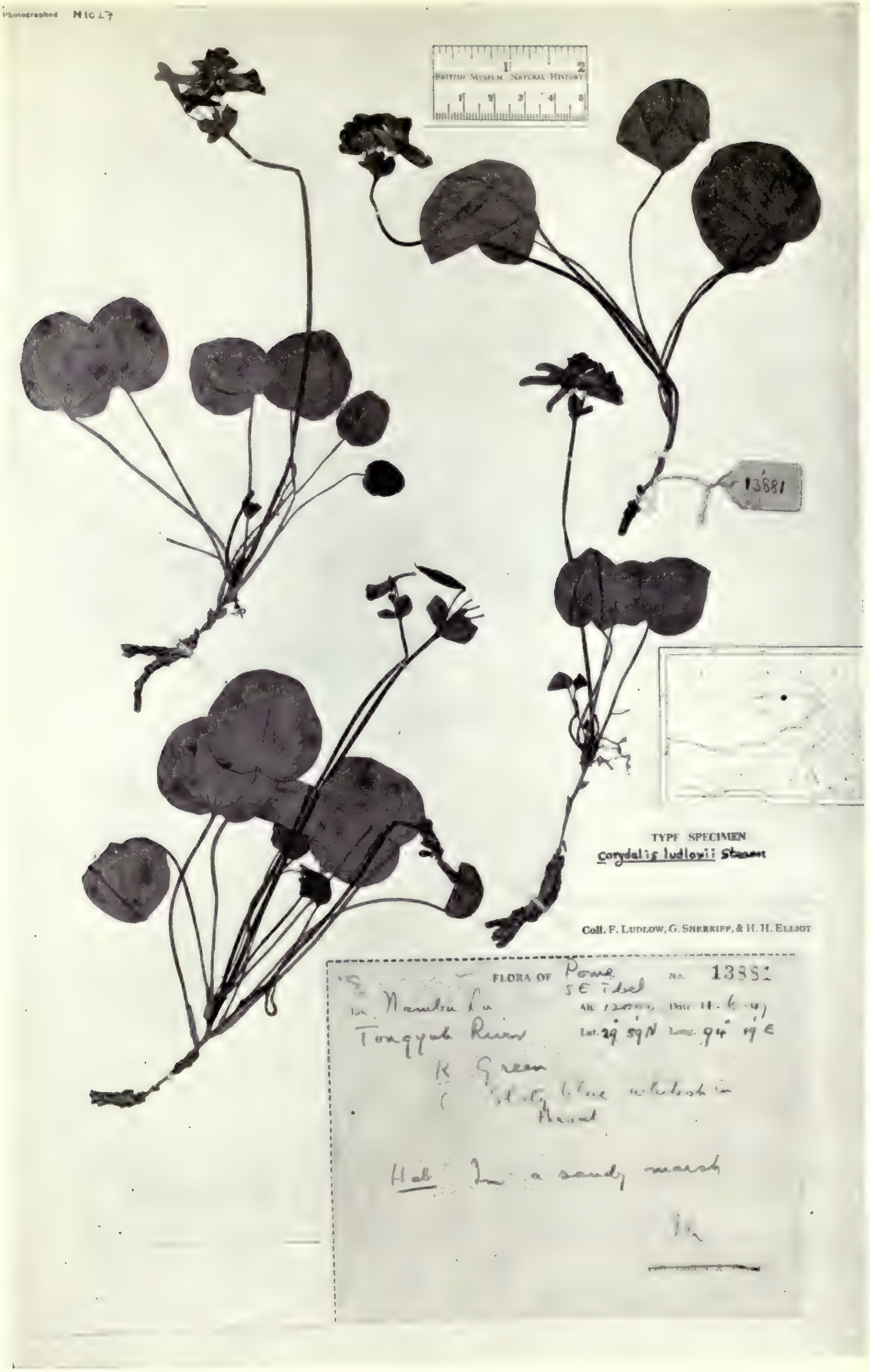
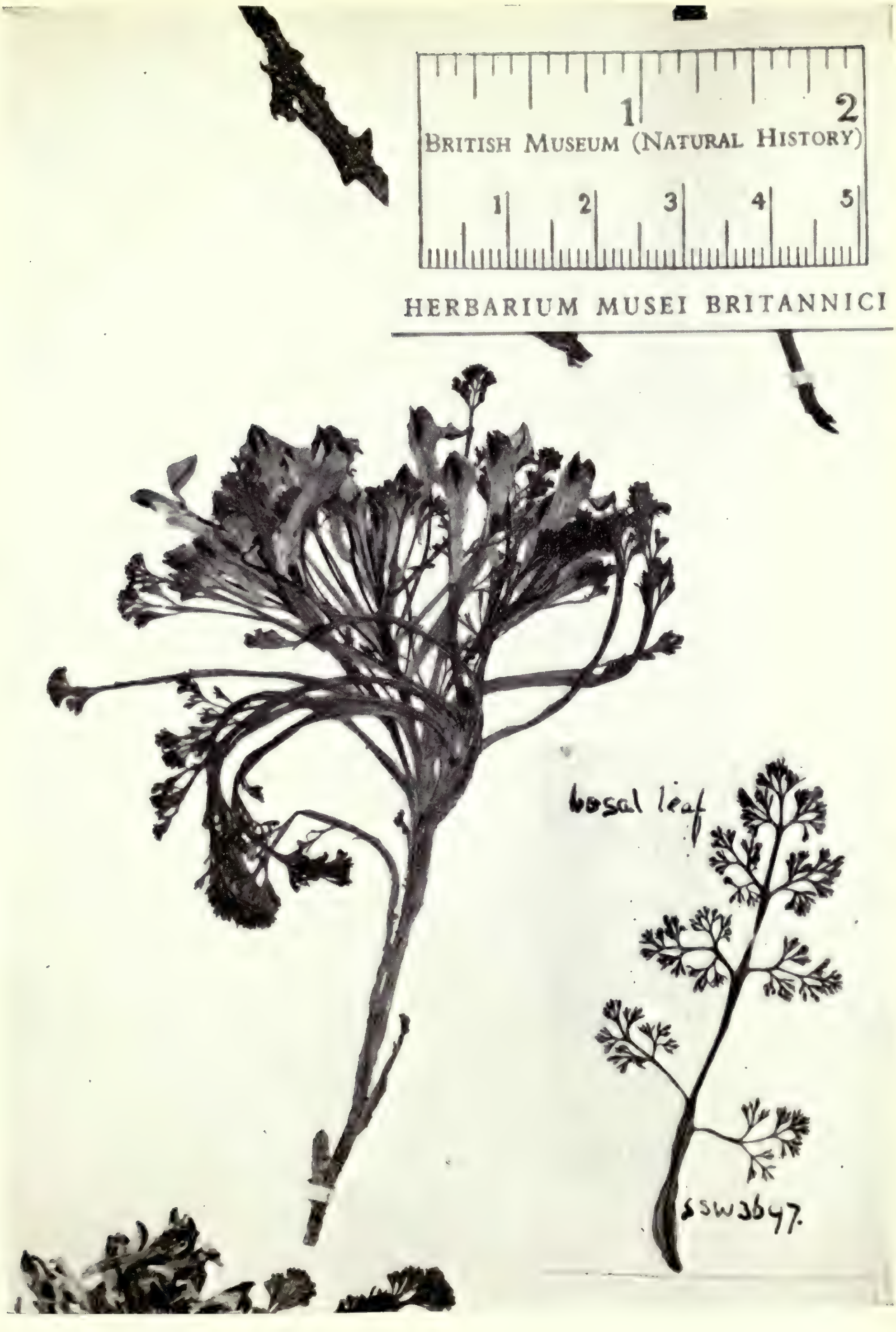

Photographed N1027
British Museum Natural History
13881
TYPE SPECIMEN
Corydalis ludlowii Stearn
Coll. F. Ludlow, G. Sherriff, & H. H. Elliot
FLORA OF Pome SE Tibet
No. 13881
Loc. Nambu La
Tongyuk River
Alt. 12000 ft Date 11.6.47
Lat. 29° 59' N Long. 94° 19' E
K Green
(Slaty blue whitish in throat
Hab. In a sandy marsh

PLATE 8

Corydalis megacalyx Ludlow (*Stainton, Sykes & Williams 3697* ; holotype)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BRITISH MUSEUM (NATURAL HISTORY)
1
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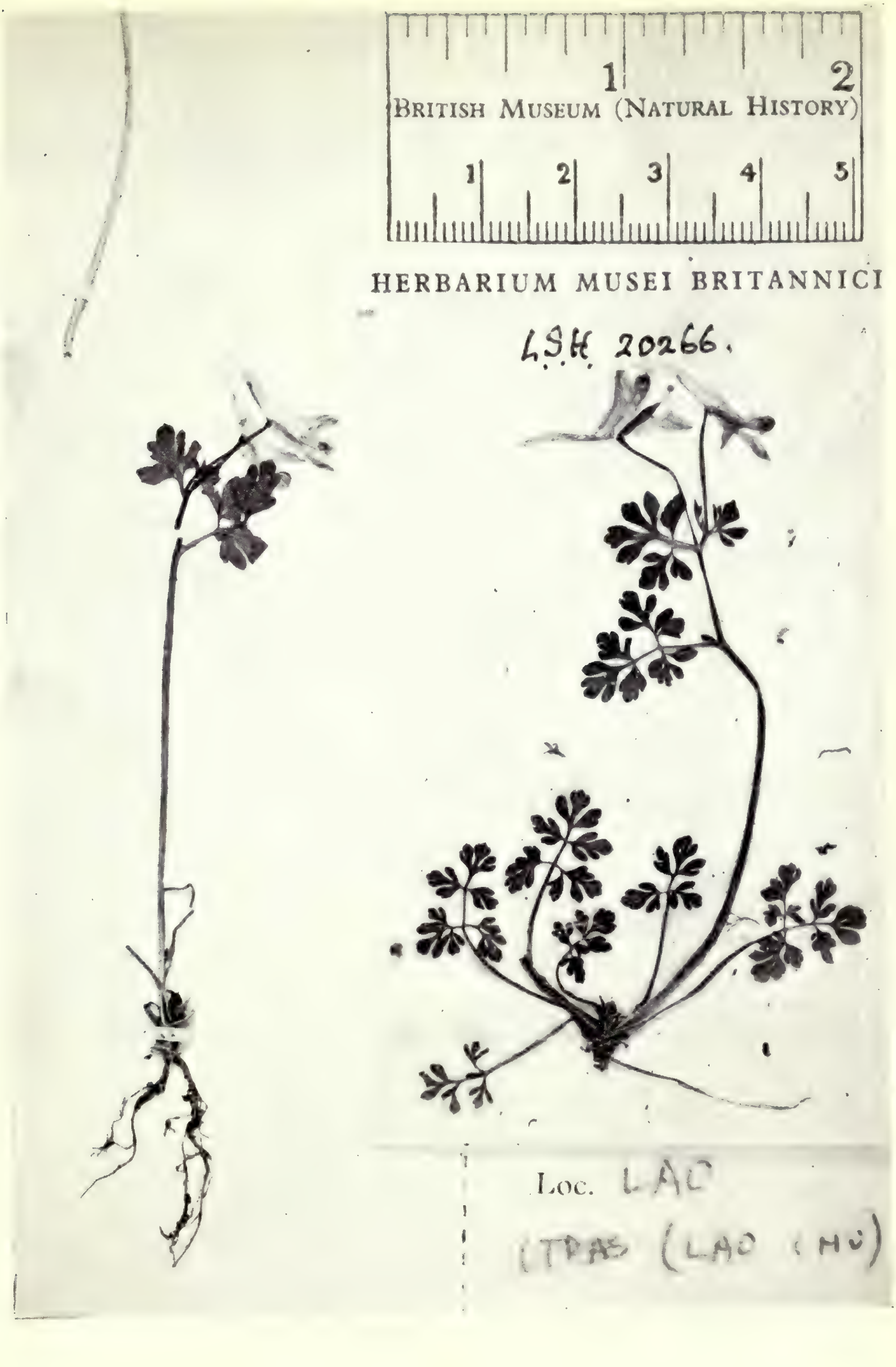
5
HERBARIUM MUSEI BRITANNICI
basal leaf
SSW3647.

PLATE 9

Corydalis oligantha Ludlow (*Ludlow, Sherriff & Hicks 20266* ; holotype)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BRITISH MUSEUM (NATURAL HISTORY)
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HERBARIUM MUSEI BRITANNICI
LSH 20266.
Loc. LAO
(TRAS (LAO CHU)

PLATE 10

Corydalis oxalidifolia Ludlow (*Ludlow, Sherriff & Hicks 20422* ; holotype)

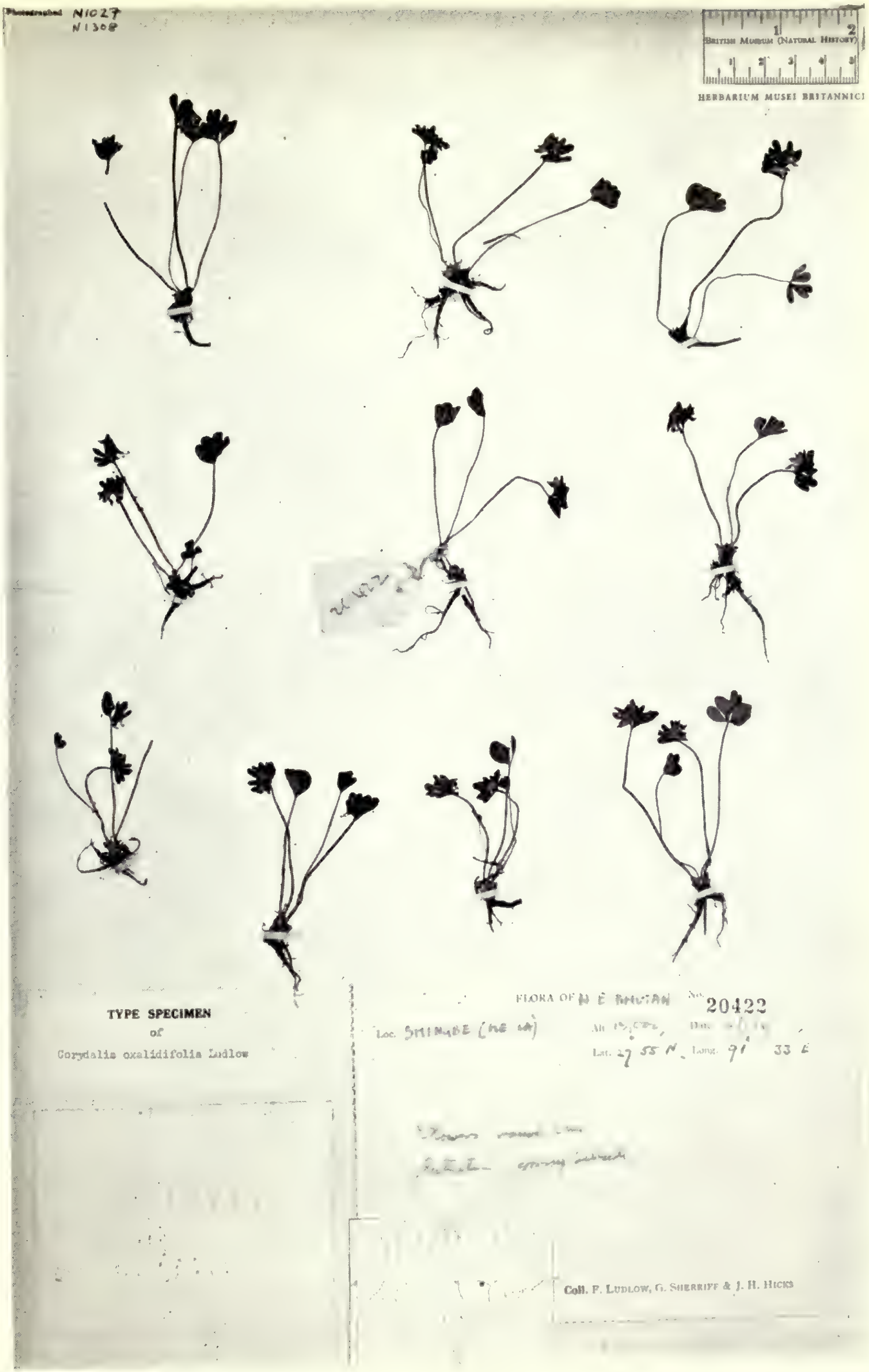
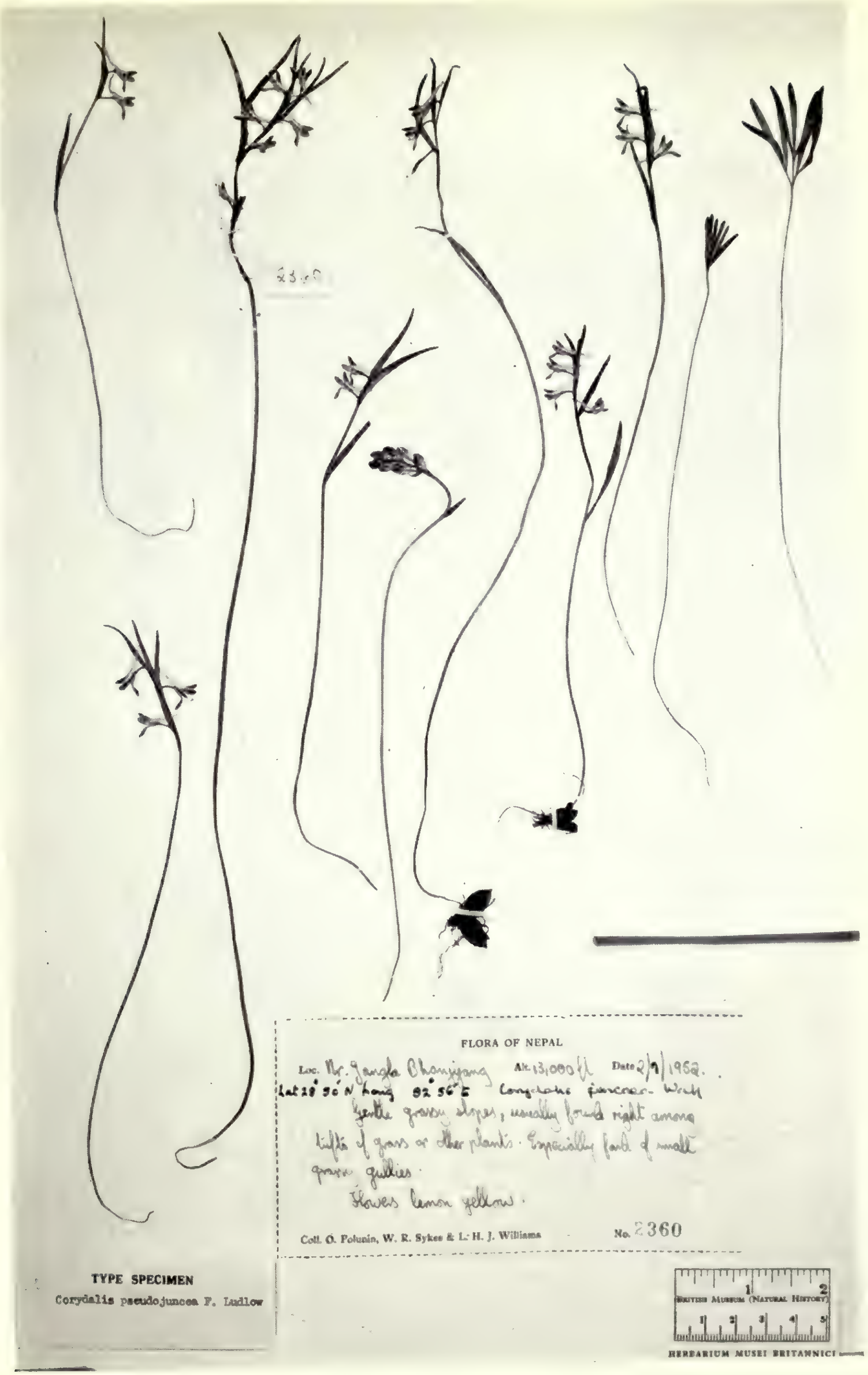

N1027
N1308
BRITISH MUSEUM (NATURAL HISTORY)
HERBARIUM MUSEI BRITANNICI
20422
TYPE SPECIMEN
of
Corydalis oxalidifolia Ludlow
FLORA OF N E BHUTAN No. 20422
Loc. SHINGBE (NE 4)
Lat. 27 55 N. Long. 91 33 E
Coll. F. LUDLOW, G. SHERRIFF & J. H. HICKS

PLATE 11

Corydalis pseudojuncea Ludlow (*Polunin, Sykes & Williams 2360* ; holotype) with *C. juncea* Wall. (central specimen in bud)



2360

FLORA OF NEPAL

Loc. Nr. Jangla Bhanjyang Alt. 13,000 ft Date 2/9/1952.
Lat 28° 50' N Long 82° 56' E Corydalis juncea Wall.
Gentle grassy slopes, usually found right among tufts of grass or other plants. Especially fond of small grassy gullies.
Flowers lemon yellow.

Coll. O. Polunin, W. R. Sykes & L. H. J. Williams No. 2360

TYPE SPECIMEN
Corydalis pseudojuncea F. Ludlow

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BRITISH MUSEUM (NATURAL HISTORY)
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HERBARIUM MUSEI BRITANNICI

PLATE 12

Corydalis quinquefoliolata Ludlow (*Ludlow, Sherriff & Taylor 5503* ; holotype)

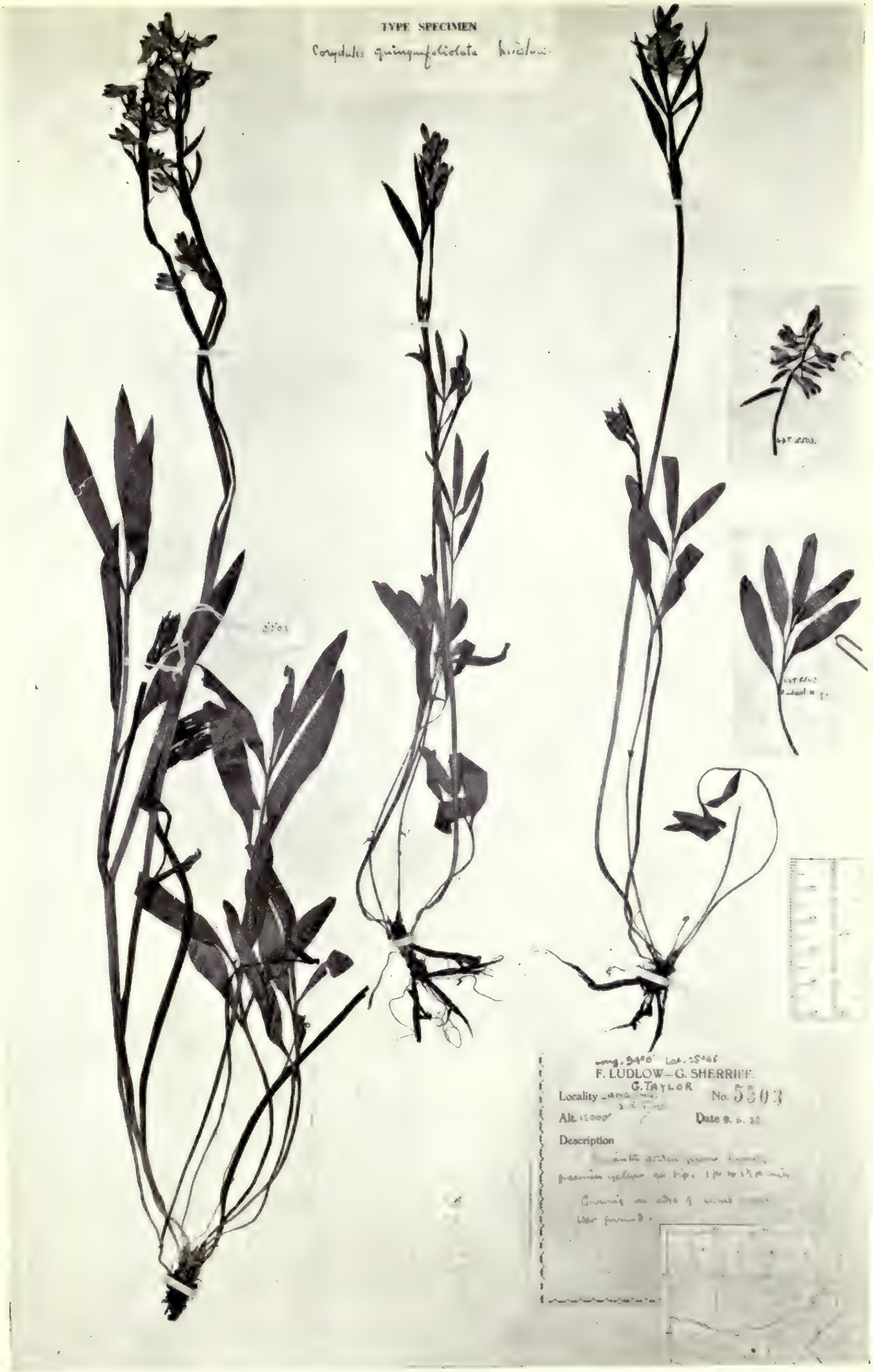

TYPE SPECIMEN
Corydalis quinquefoliolata
F. LUDLOW—G. SHERRIFF.
G. TAYLOR
Locality
No. 5503
Alt. 12000'
Date 9. 6. 38
Description

PLATE 13

Corydalis staintonii Ludlow (*Stainton 5484*; holotype)

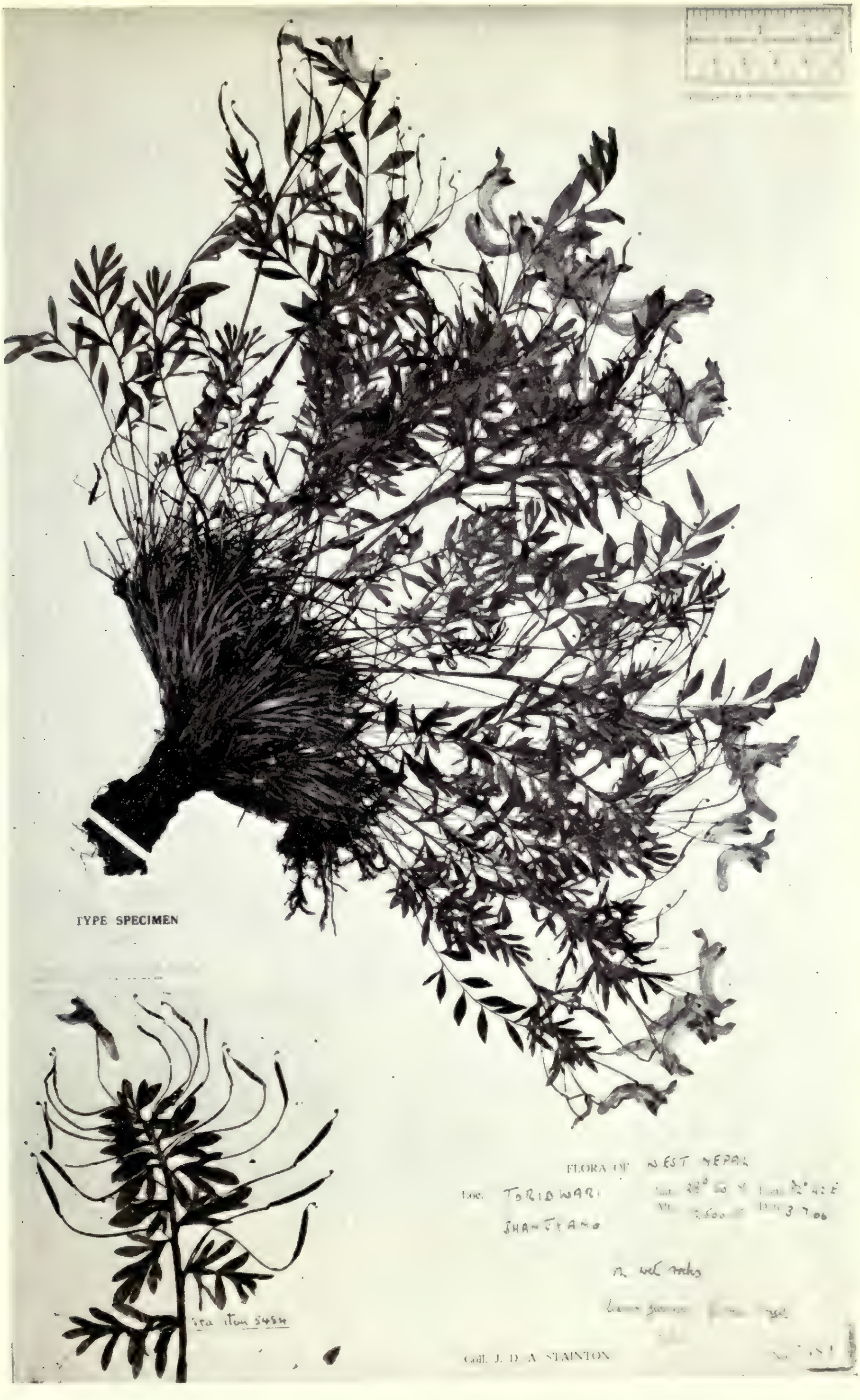

TYPE SPECIMEN
see item 5454
FLORA OF WEST NEPAL
Loc. TORIDWARI
SHANJYANG
on wet rocks
Coll. J. D. A. STAINTON

PLATE 14

Corydalis sykesii Ludlow (*Stainton, Sykes & Williams 2999* ; holotype)

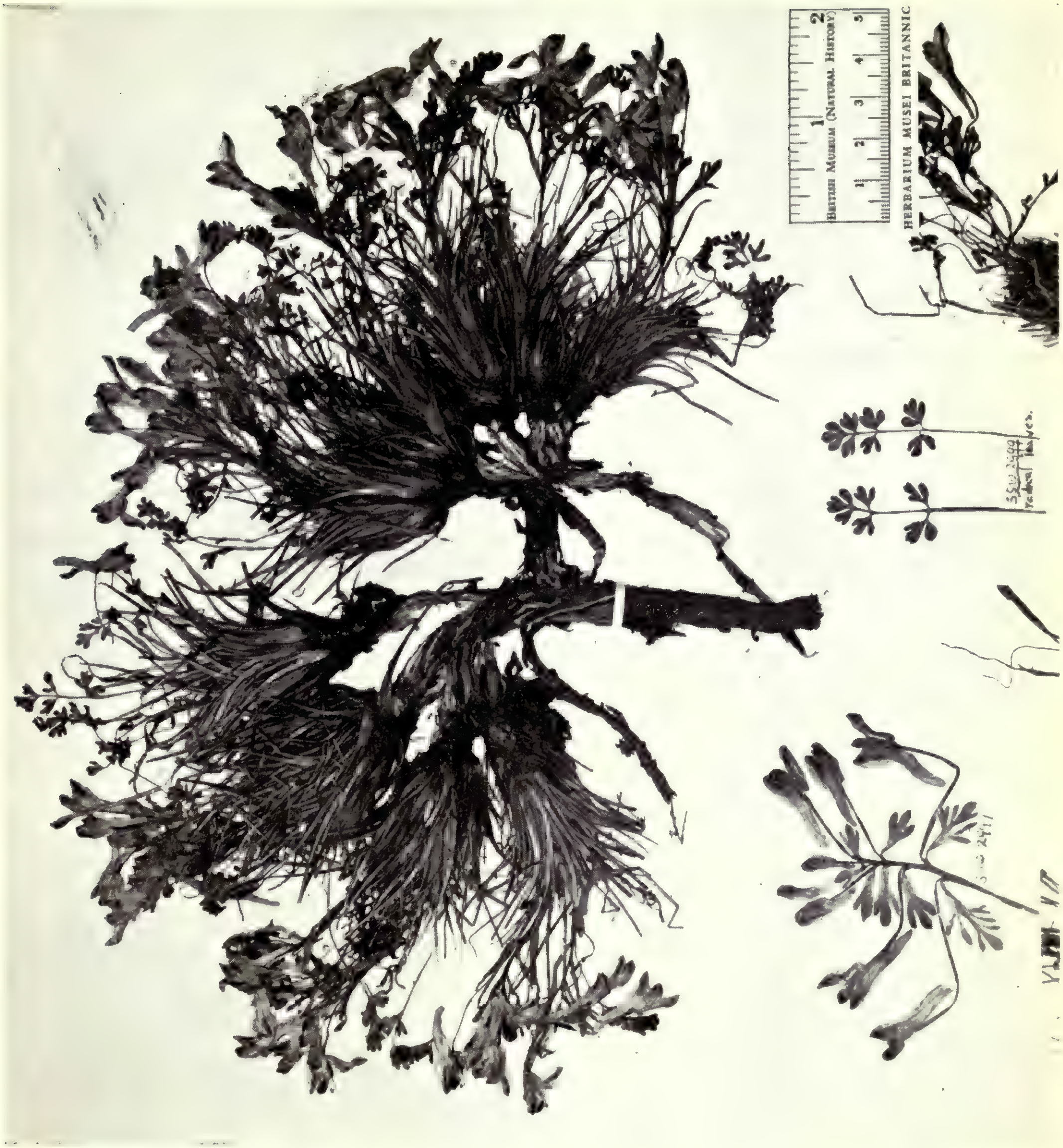
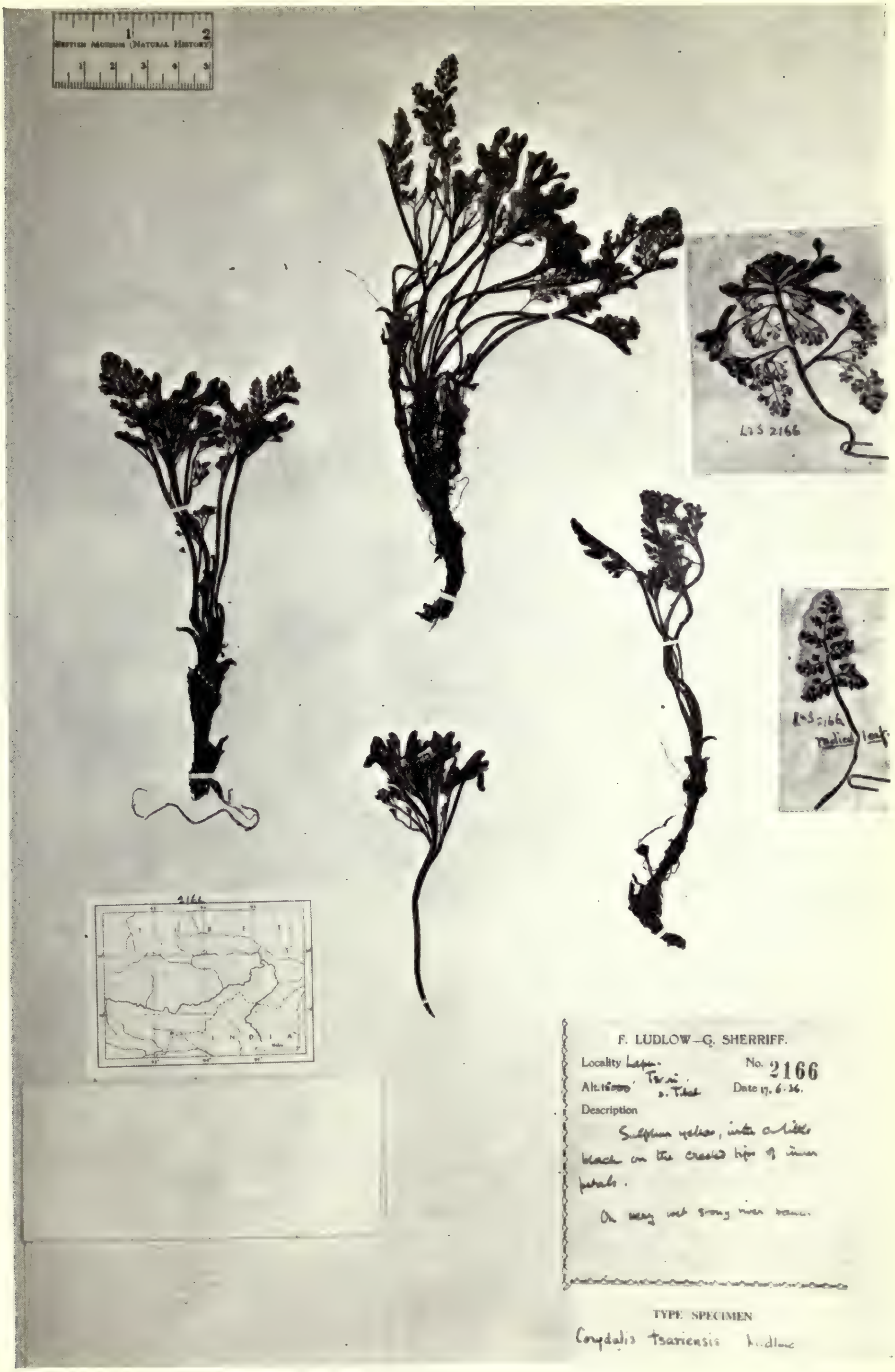

BRITISH MUSEUM (NATURAL HISTORY)
HERBARIUM MUSEI BRITANNIC

PLATE 15

Corydalis tsariensis Ludlow (*Ludlow & Sherriff 2166* ; holotype)


1
2
BRITISH MUSEUM (NATURAL HISTORY)
L&S 2166
L&S 2166 radical leaf
2166
TIBET
INDIA

F. LUDLOW—G. SHERRIFF.

Locality Lapu. Tsari. S. Tibet
No. 2166
Alt. 16000'
Date 17. 6. 36.

Description

Sulphur yellow, with a little black on the crested tips of inner petals.

On very wet stony river banks.

TYPE SPECIMEN

Corydalis tsariensis Ludlow

Printed in Great Britain by John Wright and Sons Ltd. at The Stonebridge Press, Bristol BS4 5NU

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THE MARINE ALGAE OF TRINIDAD, WEST INDIES

W. D. RICHARDSON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
BOTANY Vol. 5 No. 3
LONDON: 1975

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THE MARINE ALGAE OF TRINIDAD, WEST INDIES

BY
WALTER DUDLEY RICHARDSON
Goldsmith's College, University of London

Pp. 71–143 ; 12 *Plates* ; 2 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
BOTANY Vol. 5 No. 3
LONDON: 1975

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

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In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 5, *No.* 3, *of the Botanical series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation :
Bull. Br. Mus. nat. Hist. (Bot.)

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Issued 4 *April*, 1975 *Price* £5·20

THE MARINE ALGAE OF TRINIDAD, WEST INDIES

By W. D. RICHARDSON

SYNOPSIS

The algae described in this paper include the author's collections made during the period 1956–1962 as well as earlier collections reported in the literature or as yet unpublished. Descriptions are given for 38 Chlorophyceae, 24 Phaeophyceae and 71 Rhodophyceae. Keys to assist in identifying the genera and species of the major phyla are included. The pertinent hydrographic data for Trinidad coastal waters and details of the collecting localities are outlined. In addition to brief notes on the habitat and ecology of each species, some more general comments are made on the ecology of Trinidad marine algae.

INTRODUCTION

THE ISLAND of Trinidad, which is the southernmost of the West Indian islands, lies close to the coast of Venezuela and geographically forms part of the South American continent (Fig. 1). Although the marine algae in other parts of the Caribbean are now quite well known, thanks to W. R. Taylor's (1960) major contribution, records from Trinidad and the neighbouring coast of South America are rather scanty. The waters of the Orinoco River are discharged, through numerous estuaries, into the Gulf of Paria between Trinidad and Venezuela, and into the Atlantic to the south

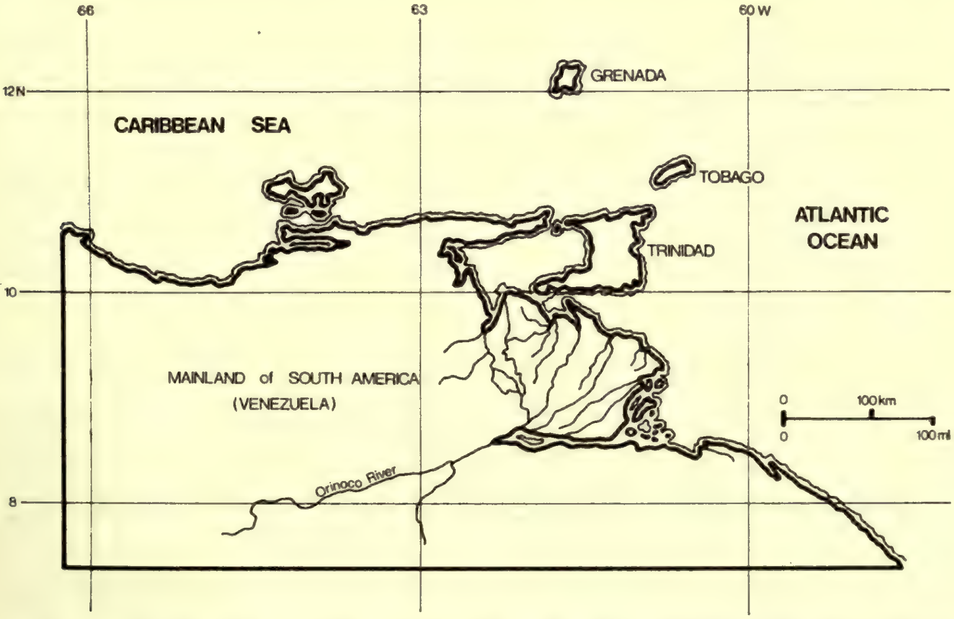

FIG. 1. The position of Trinidad in relation to the South American continent showing the main river systems which enter the sea in this area.

of Trinidad. Perhaps it has been assumed that marine algae might be considerably restricted by reduced surface salinities and the very turbid waters which flow along the coastlines in this area. However, it will be clear from this account that these waters do in fact support a marine flora which is of considerable variety and interest.

HISTORY OF TRINIDAD COLLECTIONS

The terrestrial flora of Trinidad has received the attention of many eminent botanists and, as a result, is well known. Very little attention has been given to the marine algae however. The little that is known is due to the publications of Taylor (1929, 1942, 1943, 1960). Only very few of the specimens on which these early records are based have been lodged in the Trinidad and Tobago Herbarium. Some of the oldest were collected by J. H. Hart between 1889 and 1895 when he was Director of the Botanic Gardens in Trinidad. He collected a few specimens from some of the small islets off the north-west coast. W. E. Broadway and McLean added a few more between 1893 and 1916.

The collections of Professor R. Thaxter between April 1912 and May 1913 were put on record by Taylor (1929, 1943) and included 4 Chlorophyceae, 3 Phaeophyceae and 21 Rhodophyceae. Thaxter collected from Maqueripe Bay and Manzanilla Point and there was also one specimen from an island off the north-west coast. His specimens are lodged in the Farlow Herbarium at Harvard University but no duplicates exist in Trinidad.

On a brief visit to Trinidad in April 1939 Taylor (1942) dredged for algae off Port of Spain harbour. This yielded seven more records for Trinidad, 3 Chlorophyceae, 3 Phaeophyceae and 1 Rhodophyceae. More recently R. A. Senior White in 1949, J. Bedell in 1953 and P. Tuley in 1954 sent small collections to the British Museum (Natural History) for determination. C. R. Orcutt, Bronniman and Newcombe have also made small collections. None of these specimens have been retained in the Trinidad and Tobago Herbarium.

Taylor (1960) added 6 Chlorophyceae, 3 Phaeophyceae and 15 Rhodophyceae to Trinidad records in his major work on the marine algae of the eastern tropical and sub-tropical coasts of the Americas. Thus a total of 59 species of marine algae have been recorded for Trinidad in published accounts up to 1960; this includes 13 Chlorophyceae, 9 Phaeophyceae and 37 Rhodophyceae.

1956–62 COLLECTIONS

Collections by the author of intertidal and shallow-water marine algae around the coasts of Trinidad between 1956 and 1962 have added 74 new records, bringing the totals to 38 Chlorophyceae, 24 Phaeophyceae and 71 Rhodophyceae. Dried and liquid-preserved specimens have been lodged in the Trinidad and Tobago Herbarium, which is in the care of the Botany Department of the University of the West Indies, Faculty of Agriculture, at St Augustine, Trinidad. Duplicates are lodged in the British Museum (Natural History) and a selection was sent to Professor W. R. Taylor who has kindly checked their determinations. A few duplicates were sent to the Institute of Jamaica in Kingston.

This paper places on record all the marine algae known to occur in Trinidad and describes for that area what is known of their distribution, ecology and morphology. The artificial keys and the lists of genera and species in this account follow the same arrangement as Taylor (1960).

Descriptions of orders, families and genera can be found in Taylor (1960) but are not included here. Descriptions of species which were not recorded by the author are based on those given by Taylor (1960).

Many gaps still remain in our knowledge of Trinidad marine algae. Epiphytic, crustose and calcified algae and many microscopic forms have been neglected in this work. Nor has any attempt been made to dredge or to study such special habitats as mangrove swamps, which occupy extensive areas along the east and west coasts.

DEFINITIONS

The term 'exposed' is used when referring to shores which are subjected to the physical effects of heavy wave action, while 'sheltered' refers to shores which are subjected to little or no wave action.

'Band' is used in relation to the distribution of living organisms on the shore. 'Belt' is used to refer to a part of the shore influenced by distinct physical factors.

'Littoral fringe', 'eulittoral' and 'sublittoral' are used in the sense defined by Lewis (1964) for his biological zones (bands).

Measurements of depth are expressed in metres below low water mark of ordinary spring tides.

HYDROGRAPHIC AND CLIMATIC DATA

A branch of the South Equatorial Current flows past Trinidad in a north-westerly direction, to enter the Caribbean (West Indies Pilot, Vol. 2, 1955). The flow of this current may be modified by tidal streams in inshore waters. The maximum tidal rise and fall during springs is generally a little over 0·9 m (3 ft), but it may reach 1·5 m (5 ft) near the Serpent's Mouth at the southern entrance to the Gulf of Paria (Fig. 2).

Ocean waters around Trinidad have a surface salinity of 19·2–20·0‰ Cl, but may be influenced by the flow of fresh water from the Orinoco River (Fig. 1). Salinities as low as 12‰ have been recorded in the Gulf of Paria (Andel & Postma, 1954).

The mean sea-surface temperature varies by a few degrees only, being 26 °C in February and 28 °C in August. In the Gulf of Paria these seasonal means may fluctuate by 2 °C from year to year.

The north-east trade winds, with an average speed of 3–4 knots, prevail for nine months of the year. In the three months August to October the prevailing wind is east to south-east. Thus it is the east and north coasts of Trinidad which are exposed to heavy rollers for the greater part of the year.

Inshore waters are frequently turbid, especially in the Gulf of Paria, but they are less turbid along the north coast. Oil pollution has been observed in the north of the Gulf of Paria, but is less obvious elsewhere.

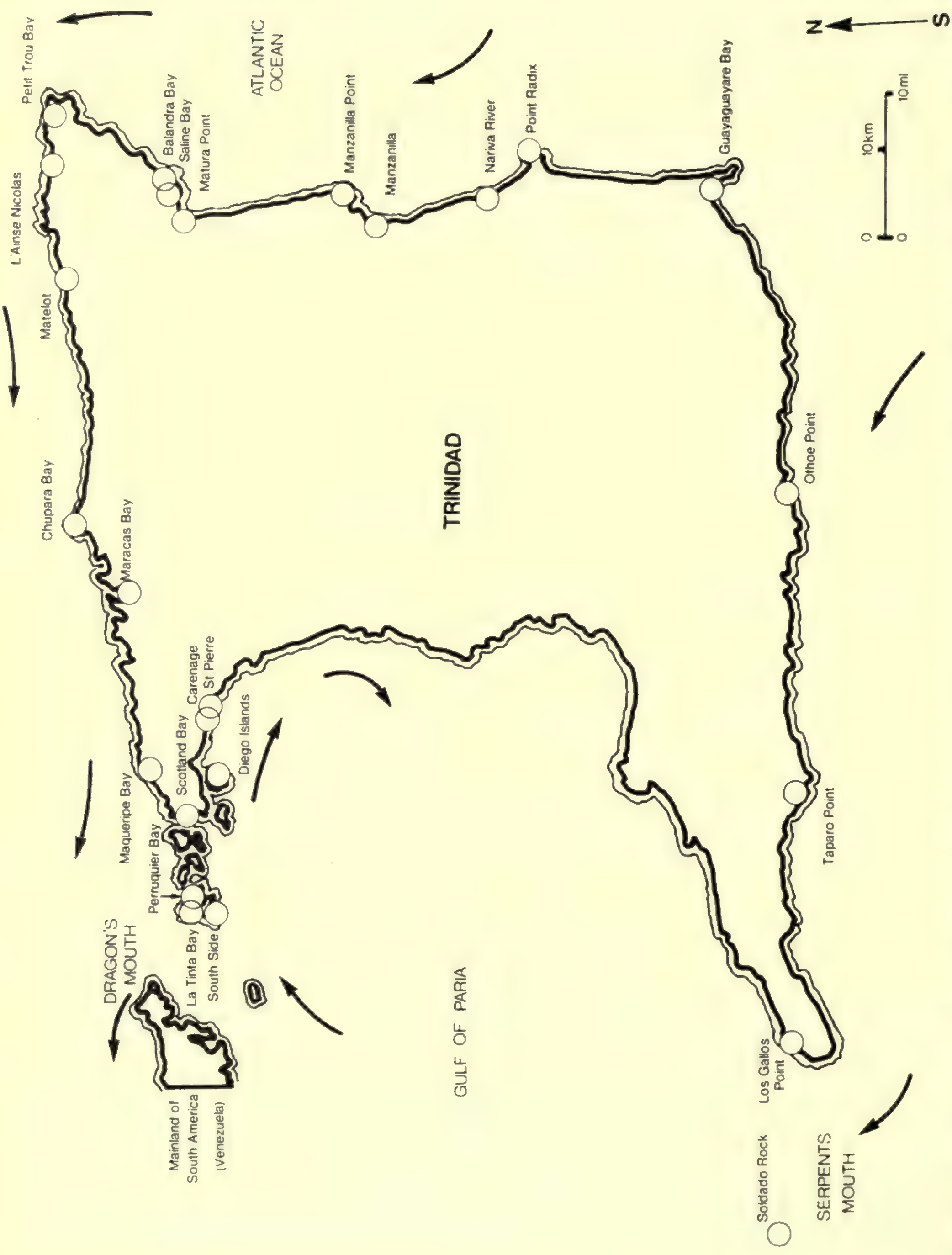
ATLANTIC OCEAN
Petit Trou Bay
Balandra Bay
Saline Bay
Matura Point
Manzanilla Point
Manzanilla
Nariva River
Point Radix
Guayaguayare Bay
N
S
0
10km
0
10mi
L'Anse Nicolas
Matelot
Chupara Bay
Maracas Bay
TRINIDAD
Othoe Point
Carenage
St Pierre
Scotland Bay
Diego Islands
Maqueripe Bay
Perruquier Bay
La Tinta Bay
South Side
DRAGON'S MOUTH
Mainland of South America (Venezuela)
GULF OF PARIA
Taparo Point
Los Gallos Point
Soldado Rock
SERPENTS MOUTH

FIG. 2. The island of Trinidad showing the stations from which collections of marine algae have been made. Arrows indicate the trend of currents, which may be considerably modified by tidal flow in inshore waters.

DESCRIPTION OF STATIONS

Particulars of the stations from which were collected the specimens on which this account is based are listed below in a geographical sequence. Where a collector is not specified, the collections were made by the author.

North Coast

Much of this rocky coast is steep, difficult of access, and exposed to heavy rollers. The offshore currents are west-going, but close inshore may be overcome by east-going tidal streams. The sea is less turbid than elsewhere around Trinidad.

1. Maqueripe Bay, 10°44′04″ N, 61°37′05″ W. Dates collected: April 1913–May 1914 (Thaxter), 15 Aug. 1957. At the head of this open bay there is a small bathing beach, and to the west of the beach a rocky area with rather sparse algal growth. Taylor (1929) recorded ten species which had been collected by Thaxter in this area.

2. Maracas Bay, 10°45′05″ N, 61°25′15″ W. Dates collected: 20 May 1956, 19 May 1962. A popular bathing beach where a few casual collections have been made from rocks at the east end of the beach.

3. Chupara Bay, 10°48′03″ N, 61°21′56″ W. Date collected: 17 June 1957. This bay lies west of the most prominent headland on the north coast and is thus sheltered from heavy rollers. A variety of algae thrived on rocky ledges and submerged rocks along the base of the cliff.

4. Matelot, 10°49′03″ N, 61°07′04″ W. Date collected: 30 July 1957. The collection area was just east of L'Islette, a group of rocks lying off-shore. The coast is very exposed, but at low water an outlying reef breaks the full force of the rollers. Algae grew abundantly on large rocks and boulders and in a few pools.

5. L'Ainse Nicolas, Toco, 10°49′45″ N, 60°59′15″ W. Date collected: 12 Aug. 1956. An exposed locality with off-shore rocks breaking the full force of the rollers. Algae were found on large stable rocks where they escaped abrasion by the many loose stones strewn over the shore.

6. Petit Trou Bay, Toco, 10°50′04″ N, 60°55′54″ W. Date collected: 23 Feb. 1960. A shallow off-shore reef was explored in this fairly sheltered locality, but turbid water made observation difficult.

East Coast

At least three-quarters of the east coast of Trinidad consists of long stretches of sandy beach. In the north, however, the coast is rocky and exposed. To the south a rocky headland lies between two long stretches of sand. The currents off this coast set north-west, following the line of the coast close inshore. Large rollers sweep the whole coastline and the water is frequently turbid.

7. Balandra Bay, 10°43′02″ N, 60°59′18″ W. Dates collected: 9 Jan. 1949 (Senior White), 1953 (Bedell), Feb. 1957, 25 Nov. 1957, 15 Mar. 1959, 22 July 1959, 16 Sept. 1959, 13 Sept. 1961. A good area for marine algae, which grew in a number of distinct habitats: rocks on the exposed shore north of the headland; on the south side of the rocky headland where it is partially sheltered; a calm, sheltered,

shallow reef in the north of the bay; sublittoral rocks and stones off the bathing beach at a depth of 1–2 m.

8. Saline Bay, 10°42′07″ N, 61°01′17″ W. Dates collected: 1 July 1957, 25 Nov. 1957, 27 Feb. 1959, 27 Mar. 1959, 24 Apr. 1959, 26 May 1959, 7 July 1959, 16 Sept. 1959, 5 Apr. 1961. A sheltered locality where there is an extensive intertidal shore and the upper sublittoral is readily accessible. There is an extensive *Sargassum* bed off-shore. A long outlying reef and rocky islet break the force of the rollers. This area was visited more frequently than any other and the algal flora is now quite well known.

9. Matura Point, 10°41′00″ N, 61°02′15″ W. Date collected: 1 July 1957. An exposed locality lying immediately south-west of the point. The eulittoral rocks were bare but some algae were found along the littoral fringe, which was wetted by wave splash, and also some stunted algal growth along the upper margin of the sublittoral.

10. Manzanilla Point, 10°31′19″ N, 61°00′45″ W. Date collected: Apr. 1912–May 1913 (Thaxter). This area was not visited by the author.

11. Manzanilla, 10°30′20″ N, 61°02′37″ W. Date collected: 18 Apr. 1939 (Taylor–Velero III, Station A36–39; Garth, 1945). Shore, estuary behind sand bar.

12. Nariva River, 10°23′40″ N, 61°01′23″ W. Date collected: 11 July 1957. A small collection from rocks and iron piles at the mouth of the river, where algal growth was influenced by fresh water.

13. Point Radix, Mayaro, 10°20′07″ N, 60°59′01″ W. Dates collected: 18 July 1957, 9 Mar. 1962. Point Radix is a prominent headland between Cocos Bay and Mayaro Bay. The collection area was on the north side of the headland, where a narrow ridge juts out at right angles to the shore line of the headland. This ridge extends northwards for about 200 m into Cocos Bay. The west side of this ridge is influenced by outflow from the Ortoire River (also known as the Guatuaro River), as evidenced by thick deposits of grey mud. The east side of the ridge faces the open sea. About 70 m along the length of this ridge is uncovered during low water springs and some good rock pools are accessible.

South Coast

Compared to the east coast, the south is much less exposed to heavy rollers. Long stretches of the shoreline are sandy but rocky areas often occur off the headlands. Between the south coast of Trinidad and the South American mainland the currents flow westward at 1·5–2 knots towards the Serpent's Mouth. Close inshore, however, tidal currents may cause an eastward flow for limited periods (Fig. 2).

14. Guayaguayare Bay, 10°08′58″ N, 61°00′56″ W. Date collected: 14 Mar. 1960. A sheltered sandy area with algae growing on scattered boulders and rocks. There were also some algae growing on the wooden breakwaters that run from high-water mark to low-water mark. The east part of the bay merits further study, and dredging or diving might prove rewarding in this area.

15. Othoe Point, 10°04′28″ N, 61°19′25″ W. Date collected: 6 Feb. 1958. Another area with scattered boulders and rocks off a headland west of Moruga.

16. Taparo Point, 10°03′09″ N, 61°38′06″ W. Date collected: July 1961. Off this point there is an extensive rocky area clearing at low water springs. The tidal rise and fall may reach 1·5 m (5 ft) in this locality. Both eulittoral and sublittoral algae were well represented.

South-west tip

Long sandy beaches extend round Icacos Point, the south-westerly tip of Trinidad. Off this point strong currents flow through the Serpent's Mouth into the Gulf of Paria.

17. Los Gallos Point, 10°04′45″ N, 61°54′15″ W. Date collected: June 1961. The seven Gallos rocks lie off this cliff headland. The shore is sandy but collections were made from the cliff face (littoral fringe), from a concrete barrier at the outlet of a small stream (eulittoral) and from a few boulders embedded in sand (sublittoral). Close inshore off this headland there are deep channels through which strong currents flow.

18. Soldado Rock, 10°04′28″ N, 62°01′00″ W. Date collected: 30 Apr. 1961. This conspicuous rock stands some 35 m high just inside the southern entrance to the Gulf of Paria. It is occupied by seabirds. The shore is only accessible near the landing point on the north-west side. A few specimens from this interesting locality were presented to the author by W. R. Dingle.

West Coast

Much of the west coast of Trinidad is unsuitable for growth of marine algae, the eulittoral being often very muddy and swampy. There are few rocky areas. No collections have been made along this coast to the south of Port of Spain, but as the coast trends westwards there are more favourable habitats for the growth of marine algae. Inshore waters in this region are influenced by tidal streams which flow westwards during ebb and eastwards during flood.

19. St Pierre, 10°40′54″ N, 61°35′38″ W. Date collected: 3 Apr. 1958. A muddy shore where a few algae grow on small muddy stones scattered within beds of *Ruppia maritima* along the upper sublittoral.

20. Carenage, 6¼ mile post, 10°40′55″ N, 61°31′03″ W. Date collected: 3 Apr. 1958. A beach of small stones extends into shallow water where it gradually disappears beneath a fine silt deposit. *Thalassia testudinum* develops on this silt. Most of the algae grew in the lower eulittoral and the upper sublittoral, but a few individuals were found at 1 m depth.

21. Carenage, west of bauxite plant, 10°41′05″ N, 61°36′07″ W. Date collected: 17 Feb. 1960. Conditions similar to the other Carenage locality.

22. Diego Islands, 10°30′39″ N, 61°37′30″ W. Date collected: 18 Apr. 1939 (Taylor–Velero III, Station A35–39; Garth, 1945). Between Diego Islands and mainland, dredged.

23. Scotland Bay, 10°42′05″ N, 61°39′42″ W. Date collected: 24 Sept. 1957. This sheltered bay lies on the north-west tip of the Trinidad mainland. Collections were made in a shoal area extending around the head of the bay. Extensive *Thalassia* beds occupy the sublittoral.

Chacachacare Island

This island is the most westerly of the group forming the Bocas del Dragon, which lie off the north-west tip of the Trinidad mainland. North- and south-going currents flow through the deep channels to the east and west of the island, the Boca de Navios and the Boca Grande. To the west, across the Boca Grande, lies the Venezuelan mainland (Fig. 2).

24. Perruquier Bay, 10°40′55″ N, 61°45′22″ W. Dates collected : 9 Mar. 1958, 31 Jan. 1960. This is a small inlet at the head of the larger Chacachacare Bay. In 1958 eulittoral and sublittoral algae were quite abundant, but in 1960 oil pollution had destroyed much of the eulittoral life. Although sheltered from rollers, the bay is open to the south-east from whence choppy seas enter with flood tides. *Thalassia* and *Ruppia* beds dominate the sublittoral flora where the bottom is silty.

25. South Side, 10°40′14″ N, 61°45′32″ W. Date collected : 12 Apr. 1961. An open stony shore, bare of algae, but with a *Sargassum* bed lying just offshore in shallow water.

26. La Tinta Bay, 10°40′53″ N, 61°45′25″ W. Dates collected : 20 Jan. 1957, 31 Jan. 1960. This bay lies on the west side of the island and is open to the Boca Grande. On the north side of the bay there are cliffs with rocky ledges lapped by the sea at their foot. On the south side of the bay, the shore is strewn with boulders. Most algae grew along the upper sublittoral and extended down to a depth of about 1 m.

The remaining stations lack precise definition. They are : Cocos Bay, 24 Mar. 1957, floating ; St Joseph, 11 July 1957, cast ; Sylvia Bay (Newcombe) ; Caledonia and Gasparee, 1893 (J. H. Hart) ; Islands (McLean).

FLORISTIC LIST

All previous records for Trinidad are given in this section, and hence those species under which no such record is cited are here recorded from the island for the first time.

CHLOROPHYCEAE

KEY TO GENERA

Thallus cellular, not composed of coenocytic filaments :
  Thallus flat, tubular or filiform, 1–2 layers of cells thick, but not a uniseriate filament :
    Thallus of adult plants tubular or filiform, 1–3 cells across 1. *Enteromorpha*
    Thallus of adult plants foliaceous :
      Adult thallus one cell layer thick . . . . . 2. *Monostroma*
      Adult thallus two cell layers thick . . . . 3. *Ulva*
  Thallus filamentous, consisting of uniseriate rows of cells :
    Filaments branched . . . . 6. *Cladophora*

Filaments unbranched or with a few short simple branches :

Filaments coarse to touch, cells barrel-shaped ; attached by a basal cell or in unattached intertwined masses . . . . . 4. *Chaetomorpha*

Filaments not coarse, cells rather long and slender ; sometimes with a few short rhizoidal branches . . . . . . 5. *Rhizoclonium*

Thallus of coenocytic filaments, which may be simple or branched or built up into a complex system (includes one calcified genus) :

Plants of obvious filamentous construction :

Original cell forming a stalk, differing from other cells . . 12. *Struvea*

Original cell not forming a stalk and similar to other cells :

Forming dense mats of entangled filaments, the lower filaments embedded in mud . . . . 16. *Boodleopsis*

Not forming dense mats nor with filaments embedded in mud :

Branching whorled or in brush-like clusters :

Branches borne in successive whorls, the first whorl arising at the apex of a single large clavate cell, the pattern being repeated (Plate 18 fig. 5) . . . . 8. *Ernodesmis*

Branches borne in brush-like cluster on upper part of original primary cell, which divides into a number of cells ; often bearing short filamentous appendages . . . . . 9. *Siphonocladus*

Branching irregular, dichotomous, or in one or two distinct rows :

Branch tips joined to one another by short disc-like attachment organs (Plate 19 fig. 1) . . . . 11. *Boodlea*

Branch tips not joined :

Plants with distinct main axes bearing one or two rows of peripheral branches of limited growth ; reproductive organs not known 13. *Bryopsis*

Plants with dichotomously branched main axes bearing numerous hair-like peripheral branches all over their surface (Plate 17 fig. 4, 5) ; reproductive organs lateral . . . 14. *Trichosolen*

Plants not of obvious filamentous construction :

Plants of simple vesicular cells or clusters of cells forming hollow sacs :

Thallus creeping but bearing some irregularly arranged erect branches ; cells large, 1–2·5 mm diam. . . . . . . 7. *Valonia*

Thallus spherical, composed of angular cells, the cell walls showing spine-like cellulose outgrowths . . . . 10. *Dictyosphaeria*

Plants of more complex form, differentiated into rhizoidal and assimilatory portions (includes calcified genus) :

Plants calcified . . . . 17. *Halimeda*

Plants not calcified :

Filaments interwoven to form spongy plants of dark green colour ; walls not supported internally by trabeculae . . . . 18. *Codium*

Filaments not interwoven, organized into rhizoidal, stoloniferous and foliar elements ; walls internally supported by trabeculae . 15. *Caulerpa*

ULVACEAE

1. *ENTEROMORPHA* Link

ENTEROMORPHA Link in C. G. Nees, Hor. Phys. Berol. : 5 (1820), *nom. cons.*

KEY TO SPECIES

Plants filiform, 1–3 cells in cross section, rarely tubular 1. *E. chaetomorphoides*
Plants tubular throughout except near the base and in filamentous proliferations :
  Plants much branched from below, the cells in surface view in marked longitudinal rows . . . . 2. *E. lingulata*
  Plants sparingly branched, the cells in longitudinal rows at the base of the branches only . . . . 3. *E. flexuosa*

1. ***Enteromorpha chaetomorphoides*** Børg. in Bot. Tidsskr. 31 : 149 (1911). (Plate 16 fig. 2.)

Plants pale green, filiform, with infrequent wide-angled branches with uniseriate tips. Axes 2–3(–5) cells wide, 45–95 μm diam. Cells 14–19 μm × 19–21 μm.

On rock faces in upper eulittoral or littoral fringe.

Los Gallos Point, June 1961, *Richardson 1077*. Scotland Bay, 24 Sept. 1957, *Richardson 215*.

From Jamaica to Brazil.

2. ***Enteromorpha lingulata*** J. Ag. in Acta Univ. lund. 19 (2) : 143 (1883).

Plants to 5 cm long, much branched from below, the branches to 2 mm wide. Cells 11–14 μm diam., in longitudinal rows.

On cliff face in littoral fringe, and on face of concrete wall in lower eulittoral. On sticks and reeds in estuary of small stream.

Manzanilla, 18–20 Apr. 1939, *Taylor 39–490* (Taylor, 1942). Los Gallos Point, June 1961, *Richardson 1071, 1072*.

Probably more widespread in Trinidad than these records suggest. It has proved difficult to determine with certainty.

From North Carolina to Brazil.

3. ***Enteromorpha flexuosa*** (Roth) J. Ag. in Acta Univ. lund. 19 (2) : 126 (1883).

Conferva flexuosa Roth, Cat. Bot. 2 : 188 (1800).
Ulva flexuosa (Roth) Wulf. in Arch. Bot., Leipzig 3 : 1 (1803) ; reimpr. ut Crypt. Aquat. : 1 (1803).

To 12 cm tall, sparingly branched below (2–4 branches). Branches to 3 mm near tips, tapering to 0·1 mm at base. Cells to 24 μm diam. in longitudinal rows at base of branches but irregular near branch tips.

On south coast, on rocks and in tide pools, lower eulittoral.

Guayaguayare Bay, 14 Mar. 1960, *Richardson 1004*. Taparo Point, July 1961, *Richardson 1086, 1106*.

From Bermuda to Brazil.

2. *MONOSTROMA* Thuret

MONOSTROMA Thuret in Mém. Soc. Sci. nat. Cherbourg 2 : 29 (1854).

1. ***Monostroma oxyspermum*** (Kütz.) Doty in Farlowia 3 : 12 (1947). (Plate 16 fig. 1.)

Ulva oxysperma Kütz., Phyc. Gen. : 296 (1843).

Thallus bright to dark green, soft, slimy, and crumpled irregularly, 3–5 cm tall, 25–40 μm thick, and of only one cell layer. In transverse section cells 14 μm long, with thick gelatinous walls. In surface view, cells in groups of 2–4, each cell 8–14 μm diam.

In sheltered localities, on rocks, coconut stumps and concrete walls in mid or upper eulittoral.

Guayaguayare Bay, 14 Mar. 1960, *Richardson 491, 496*. Los Gallos Point, June 1961, *Richardson 1069*.

From Bermuda to Florida, Brazil.

3. *ULVA* L.

ULVA L., Sp. Pl. 2 : 1163 (1753) ; Gen. Pl., ed. 5 : 492 (1754), *nom. cons.*

KEY TO SPECIES

Plants divided into narrow segments, to 3 cm broad ; in transverse section the cells of the midline region taller than those at the margin . 2. *U. fasciata*

Plants simple or with broad lobes ; in transverse section the cells usually square 1. *U. lactuca*

1. ***Ulva lactuca*** L., Sp. Pl. 2 : 1163 (1753).

Recorded by Taylor (1960).

From Bermuda to Brazil.

2. ***Ulva fasciata*** Delile, Fl. Égypte : 297 (1813).

Frond crisp, clear green, with undulate margins. Linear lobes to 50 cm long, but shorter and broader in sheltered localities. Lobes to 120 μm thick, of two layers of cells. In surface view cells 25–32 μm × 14–23 μm.

On rocks from lower eulittoral to sublittoral, eastern part of north coast of Trinidad ; also known from Tobago.

Chupara Bay, 17 June 1957, *Richardson 73*. Matelot, 30 July 1957, *Richardson 147*. L'Ainse Nicolas, 12 Aug. 1956, *Richardson 9*. Petit Trou Bay, 23 Feb. 1960, *Richardson 485*.

From Bermuda to Brazil.

CLADOPHORACEAE

4. *CHAETOMORPHA* Kütz.

CHAETOMORPHA Kütz., Phyc. Germ. : 203 (1845), *nom. cons.*

KEY TO SPECIES

Filaments without clear basal attachment . . . . . . 1. *C. crassa*
Filaments clearly basally attached :
  Main filaments broadening towards their apices . . . . 4. *C. clavata*
  Main filaments not broadening towards their apices :
    Plants forming dense tufts, basal cells more than 4 mm long, filaments more than 400 μm diam. . . . . 3. *C. antennina*
    Plants not in dense tufts, basal cells less than 2 mm long, filaments less than 400 μm diam. . . . . 2. *C. linum*

1. ***Chaetomorpha crassa*** (Ag.) Kütz., Phyc. Germ. : 204 (1845). (Plate 16 fig. 6.)

Conferva crassa Ag., Syst. Alg. : 99 (1824).

Filaments 270–675 μm diam., cells 0·5–2·0 times their diameter in length. No evident basal attachment.

Coarse, wiry filaments entangled with other algae (*Sargassum* and *Hypnea*) at about 1 m depth.

Guayaguayare Bay, 14 Mar. 1960, *Richardson 1003*. Soldado Rock, 30 April 1961, *Richardson 1056*.

From Bermuda to St Barthelemy, now extended to Trinidad.

2. ***Chaetomorpha linum*** (O. F. Müll.) Kütz., Phyc. Germ. : 204 (1845). (Plate 16 fig. 3.)

Conferva linum O. F. Müll, in Oeder, Ic. Pl. Sponte Nasc. Dan. & Norv., Fl. Dan. 5 (13) : 7, t. 771 (1778).
Conferva aerea Dillw., Brit. Confervae : t. 80 (1806).
Chaetomorpha aerea (Dillw.) Kütz., Sp. Alg. : 379 (1849).

Filaments less than 20 cm (–30 cm) long. Basal cells 0·5–1·5 mm long, 65–160 μm diam. near tips, 3·5–11·5 times as long as their diameter, attached to substrata. Suprabasal cell 200–565 μm long × 105–235 μm diam. Filaments not exceeding 400 μm diam., most cells 1–2·5 times as long as their diameter.

On rocks, in pools, or embedded in sand, upper eulittoral.

Saline Bay, 1 July 1957, *Richardson 80* ; 25 Feb. 1957, *Richardson 240* ; 27 Feb. 1959, *Richardson 327* ; 27 Mar. 1959, *Richardson 395*. Taparo Point, July 1961, *Richardson 1105*.

From Bermuda to Virgin Isles, Brazil.

3. ***Chaetomorpha antennina*** (Bory) Kütz., Sp. Alg. : 379 (1849). (Plate 16 fig. 4.)

Conferva antennina Bory, Voy. Mers Afr. Le Naturaliste 2 : 161 (1804).
Conferva media Ag., Syst. Alg. : 100 (1824).
Chaetomorpha media (Ag.) Kütz., op. cit. : 380 (1849).

Tufts 3–13 cm tall, with long, clavate basal cells 4–10 mm long. Filaments 400–800 μm diam., cells 1–2 times as long as broad.

Priority requires that the name *C. antennina* be used for this species rather than *C. media*, which Taylor (1960) adopts for it.

Inconspicuous plant of upper sublittoral.

Maqueripe Bay, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929, as *Chaetomorpha media*). Maracas Bay, 20 May 1956, *Richardson 3*. Chupara Bay, 17 June 1957, *Richardson 68*. L'Ainse Nicolas, 12 Aug. 1956, *Richardson 10*. Balandra Bay, 22 July 1959, *Richardson 441*. Manzanilla Point, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929, as *Chaetomorpha media*).

From Bermuda to Brazil.

4. ***Chaetomorpha clavata*** (Ag.) Kütz. in Bot. Ztg 5 : 166 (1847). (Plate 16 fig. 5.)

Conferva clavata Ag., Syst. Alg. : 99 (1824).

Filaments wiry, entangled, reaching 10–15 cm in length, attached by clavate basal cell, 1·2–1·4 mm long, 3·5–4·5 times as long as its diameter and 2–3 times the length of the suprabasal cell. Filaments increase in diameter from about 290 μm below to 690 μm above. Lower cells slightly longer than their diameter but upper cells shorter.

Sublittoral at 0·5 m depth, and eulittoral pool.

Balandra Bay, 15 Mar. 1959, *Richardson 364*. Taparo Point, July 1961, *Richardson 1112*.

From Florida to Brazil.

5. ***RHIZOCLONIUM*** Kütz.

RHIZOCLONIUM Kütz., Phyc. Gen. : 261 (1843).

1. ***Rhizoclonium riparium*** (Roth) Harv., Phyc. Brit. : t. 238 (1849).

Conferva riparia Roth, Cat. Bot. 3 : 216 (1806).

Dr J. T. Koster, who has kindly checked this material, recognizes two forms in the Trinidad specimens. A complete synonymy has been published by her (Koster, 1955), but I have indicated here the synonyms under which these two forms are described by Taylor (1960).

1a. ***Rhizoclonium riparium*** forma ***riparium***

Rhizoclonium riparium [var.] γ ***implexum*** Rosenv. in Meddr. Grønland 3 : 915 (1893) pro parte, non *Conferva implexa* Dillw.

Filaments 20–26 μm diam., cells 1·5–3·0 times as long as their diameter.

On rock faces in upper eulittoral.

Point Radix, 18 July 1957, *Richardson 144*.

1b. ***Rhizoclonium riparium*** forma ***validum*** Foslie in Wittr. & Nordst., Alg. Exsicc. : no. 624 (July 1884) ; in Bot. Notiser 1884 : 125 (Sept. 1884). (Plate 18 fig. 2.)

Conferva tortuosa Dillw., Brit. Confervae : t. 46 (1805).
Rhizoclonium tortuosum (Dillw.) Kütz., Phyc. Germ. : 205 (1845).

Filaments (35–)41–49(–55) μm diam., cells 1·5–3·0(–5·0) times as long as their diameter. Rhizoidal branches infrequent.

On large rocks in upper sublittoral.

Othoe Point, 6 Feb. 1958, *Richardson 249*.

The species as a whole occurs from Bermuda to Brazil.

6. *CLADOPHORA* Kütz.

CLADOPHORA Kütz., Phyc. Gen. : 262 (1843), *nom. cons.*

KEY TO SPECIES

Densely matted, forming moss-like turf . . . . 1. *C. coelothrix*
Not densely matted :
  Plants coarse and stiff, old parts of main axes more than 300 μm in diam. 4. *C. prolifera*
  Plants soft and delicate, old parts of main axes less than 300 μm in diam. :
    Main axes more than 150 μm diam., light green . . 3. *C. fascicularis*
    Main axes less than 60 μm diam., dark green . . 2. *C. delicatula*

1. ***Cladophora coelothrix*** Kütz., Phyc. Gen. : 272 (1843). (Plate 17 fig. 3.)

Conferva repens J. Ag., Alg. Maris Medit. & Adriat. : 13 (1842), non *Conferva repens* Dillw. (1802).
Cladophora repens Harv., Phyc. Brit. : t. 236 (1849).

Branches infrequent, filaments 80–115 μm diam. Cells 6–11 times as long as their diameter.

C. coelothrix Kütz. is the earliest legitimate name for this species, *Conferva repens* J. Ag. being a later homonym.

Thick moss-like tufts on rock faces and beneath overhanging ledges in upper eulittoral and littoral fringe.

Point Radix, 18 July 1957, *Richardson 146*. Perruquier Bay, 9 Mar. 1958, *Richardson 294*.

Bermuda to Panama.

2. **Cladophora delicatula** (Mont.) Kütz., Tab. Phyc. 6 : 1, t. 1 fig. II (1856).

Conferva delicatula Mont. in Annls Sci. nat., ser. 3, Bot. 14 : 302 (1850).

Delicate, soft, dark green filaments to 10 cm long. Filaments bear short erect branches usually less than 9 cells long. Main axis 25–60 μm diam., cells (1·0–)2·0–2·5(–5·0) times as long as their diameter.

In shallow pools and on small stones, upper eulittoral.

Saline Bay, 27 Feb. 1959, *Richardson 328a*; 27 Mar. 1959, *Richardson 391, 392*; 5 Apr. 1961, *Richardson 1040*. Taparo Point, July 1961, *Richardson 1107, 1111*.

From Bermuda to French Guiana.

3. **Cladophora fascicularis** (Mert. ex Ag.) Kütz., Phyc. Gen. : 268 (1843). (Plate 17 fig. 2.)

Conferva fascicularis Mert. ex Ag., Syst. Alg. : 114 (1824).

Trinidad specimens are smaller than reported by Taylor (1960). Plants 4–6(–10) cm tall, tufted, light green. Older axes 150–275 μm diam., the cells 4–6 times as long as their diameter. Peripheral branches 30–118 μm diam., less than 1·5 cm long and consisting of 3–7 cells, each 2–3 times as long as their diameter.

On small rocks along upper sublittoral and down to a depth of 0·5 m in *Sargassum* beds, one specimen embedded in sand in upper eulittoral.

Saline Bay, 1 July 1957, *Richardson 89*; 27 Mar. 1959, *Richardson 379*; 26 May 1959, *Richardson 394*; 7 July 1959, *Richardson 410*; 5 Apr. 1961, *Richardson 1039*.

From Bermuda to Brazil.

4. **Cladophora prolifera** (Roth) Kütz., Phyc. Germ. : 207 (1845). (Plate 17 fig. 1.)

Conferva prolifera Roth, Cat. Bot. 1 : 182 (1797).

Plants dark green, coarse and to 12 cm tall. Filaments attached by rhizoids which develop from basal cell. Lower cells to 475 μm diam., often more than 10 times as long. Filaments branch profusely above, the peripheral branches being 150–275 μm diam.

Sublittoral, 0·5 m depth.

Saline Bay, 1 July 1957, *Richardson 92*; 5 Apr. 1961, *Richardson 1038*. Othoe Point, 6 Feb. 1958, *Richardson 268*. Taparo Point, July 1961, *Richardson 1101*. Apr. 1912–May 1913, *Thaxter* (Taylor, 1929).

From Bermuda to Brazil.

5. **Cladophora trinitatis** Kütz., Sp. Alg. : 420 (1849).

Listed as an uncertain record by Taylor (1960). Trinidad is the type locality.

VALONIACEAE

7. *VALONIA* Ag.

VALONIA Ag., Sp. Alg. 1 : 428 (1822).

This generic name is often attributed to Ginnani (Opere Postume 1 : 38 (1755)), but all the other names in this work are vernacular Italian, and 'Valonia' therein must also be so regarded.

1. ***Valonia utricularis*** (Roth) Ag., Sp. Alg. 1 : 431 (1822).

Conferva utricularis Roth, Cat. Bot. 1 : 160 (1797).

Not recorded by the author. Description based on Taylor (1960).

Plants attached, creeping, becoming erect to 5 cm tall, composed of short filaments of large cells, 1·0–2·5 mm diam., 5–20 mm long.

Sublittoral, 3–5 m depth.

Diego Islands, 18 Apr. 1939, *Taylor 39–489b* (Taylor, 1942).

From Bermuda to Panama, Trinidad and Brazil.

8. *ERNODESMIS* Børg.

ERNODESMIS Børg. in Bot Tidsskr. 32 : 259 (1912).

1. ***Ernodesmis verticillata*** (Kütz.) Børg. in Bot. Tidsskr. 32 : 259 (1912). (Plate 18 fig. 5.)

Valonia verticillata Kütz., Sp. Alg. : 508 (1849).

Small light green tufts, 2–4 cm tall. These plants agree closely with Børgesen's (1913) description of this species. Rhizoids septate, 100–200 μm diam., the clavate basal cell annulate below, 0·9–1·3 mm diam. and 6·5–10·0 mm long. Basal cell bears a cluster of branches which reach a similar diameter.

On rocks in lower eulittoral and the sublittoral fringe.

Balandra Bay, Feb. 1957, *Richardson 52*. Saline Bay, 27 Feb. 1959, *Richardson 349, 356*. Point Radix, 9 Mar. 1962, *Richardson 1133*.

From Bermuda to Brazil.

9. *SIPHONOCLADUS* Schmitz ex Hauck

SIPHONOCLADUS Schmitz ex Hauck in Rabenh., Krypt.-Fl. Deutschl., Osterr. & Schweiz, 2 Aufl., 2 : 470 (1885).

Siphonocladus Schmitz in Ber. Sitz. naturf. Ges. Halle 1878 : 20 (1879), ***nom. nud.***

1. ***Siphonocladus tropicus*** J. Ag. in Acta Univ. lund. 23 (2) : 105 (1887). (Plate 18 fig. 4.)

Light green tufts to 4 cm long, the axes not more than 1 mm diam. Primary cell annulate below, becoming divided into many cells above, bearing many long slender branches of similar form on the surface. Third-degree branches of limited growth, borne on some of the long slender branches.

Cast on shore at Balandra Bay.

Balandra Bay, 4 Aug. 1959, *Richardson 458.*

From Bermuda to Tobago.

10. ***DICTYOSPHAERIA*** Decaisne ex Kütz.

DICTYOSPHAERIA Decaisne ex Kütz., Sp. Alg. : 512 (1849).

Dictyosphaeria Decaisne in Annls Sci. nat., ser. 2, Bot. 17 : 328 (1842), *nom. nud.*

1. ***Dictyosphaeria*** sp.

Cushions to 2 cm diam., the polygonal segments generally less than 2 mm diam. On inside of segment walls are straight simple spines, 55–105 μm long and 8–16 μm diam. Lenticular cells without haptera, ovoid and approximately 40 × 50 μm.

Growing with *Caulerpa racemosa* at depth of 0·5 m.

Petit Trou Bay, 23 Feb. 1960, *Richardson 490.*

This specimen seems to agree with descriptions of *D. versluysii* Weber-van Bosse (Egerod, 1952). Taylor (1960) records *D. vanbosseae* Borg., which may prove to be a small variety of *D. versluysii*, from Jamaica and the Virgin Islands. On the other hand, *Richardson 490* is not unlike *Valonia ocellata* Howe, which, as Taylor (1960) points out, is exceedingly difficult to distinguish from young, ill-formed plants of *Dictyosphaeria.*

11. ***BOODLEA*** Murray & De Toni

BOODLEA Murray & De Toni in J. Linn. Soc., Bot. 25 : 245 (1889).

1. ***Boodlea struveoides*** Howe in N. L. Britton, Fl. Bermuda : 496 (1918). (Plate 18 fig. 1, Plate 19 fig. 1.)

Stipe composed of one long basal cell, 2·5–5·5 mm long and 250–400 μm diam. Main axes, where distinguishable in the lower part of the plant, 230–260 μm diam. and 3·5–4·5 times as long. Branches usually opposite, their terminal cells 65–130 μm diam. The entangled branch tips joined by short disc-like holdfasts.

Light green, entangled mats on rocks in shallow water.

Saline Bay, 24 Apr. 1959, *Richardson 388.*

From Bermuda to Trinidad.

12. ***STRUVEA*** Sonder

STRUVEA Sonder in Bot. Ztg. 3 : 49 (1845).

1. ***Struvea anastomosans*** (Harv.) Piccone, Croc. Corsaro Madera & Canarie, Alghe : 20 (1884). (Plate 18 fig. 3.)

Cladophora anastomosans Harv., Phyc. Austral. 2 : t. 101 (1859).

Thallus 1–3(–5) cm tall. Stipe 0·5–1·5 cm long and 600–700 μm diam. Lamina a network of filaments 2 cm tall and 1·5 cm broad, the branching opposite, tripinnate or quadripinnate.

In small clumps from lower eulittoral into the sublittoral. Often inconspicuous, sometimes epiphytic on other algae, usually mixed with dense tufted species on rock faces.

Saline Bay, 1 July 1957, *Richardson 102*; 27 Feb. 1959, *Richardson 351*. Othoe Point, 6 Feb. 1958, *Richardson 272*. Unknown locality, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929).

From Florida to Trinidad.

BRYOPSIDACEAE

13. ***BRYOPSIS*** Lamour.

Bryopsis Lamour. in Nouv. Bull. Soc. philom. Paris 1 : 333 (1809).

Key to Species

Peripheral branches borne all around the main axes . . . 3. *B. halliae*

Peripheral branches borne in one row or two opposite rows on the main axes:

- Plants light to olive green, peripheral branches in two rows on main axes, the complete fronds triangular to lanceolate in outline. Main axes usually more than 400 μm diam. . . . . 1. *B. plumosa*
- Plants dark green, peripheral branches in one or two rows on the main axes, the complete fronds linear-lanceolate in outline. Main axes usually less than 400 μm diam. . . . . 2. *B. pennata*

1. ***Bryopsis plumosa*** (Huds.) Ag., Sp. Alg. 1 : 448 (1822).

Ulva plumosa Huds., Fl. Angl., ed. 2 : 571 (1778).

To 10 cm tall, the main axes 390–500 μm diam., naked below for 1·0–1·5 cm, but bearing distichous peripheral branches of limited growth along the rest of their length. Peripheral branches 60–130 μm diam., 1·0–1·8 mm long, tapering from the longest branches below to the shortest near the apex. The width of the whole frond 0·2–1·0 cm.

Olive-green plants from upper sublittoral and lower eulittoral rock pools.

Saline Bay, 27 Mar. 1959, *Richardson 366*. La Tinta Bay, 20 Jan. 1957, *Richardson 31*.

From Bermuda to British Honduras, Brazil.

2. ***Bryopsis pennata*** Lamour. in Nouv. Bull. Soc. philom. Paris 1 : 333 (1809).

Main axes 210–400 μm diam., peripheral branches 80–150 μm diam. and to 2 mm long. Frond to 0·6 cm in maximum diameter. The Trinidad specimens are probably var. *leprieurii* (Kütz.) Coll. & Herv. (Proc. Am. Acad. Arts Sci. 53 : 62 (1917)).

It has proved difficult to distinguish between *Bryopsis plumosa* and *B. pennata* in Trinidad specimens.

Plants dark green on rocks along upper sublittoral.

Balandra Bay, 15 Mar. 1959, *Richardson 362*. La Tinta Bay, 31 Jan. 1960, *Richardson 469*. Also recorded by Taylor (1960).

From Bermuda to Brazil.

3. ***Bryopsis halliae*** W. R. Tayl. in Phycologia 2 : 26 (1962).

Bryopsis duchassaingii sensu Schramm & Mazé, Essai Class. Algues Guadel. : 45 (1865) ; op. cit., ed. alt. : 110 (1866) ; op. cit., ed. 2 : 101 (1870–77), non J. Ag.—Collins in Tufts Coll. Stud. 2 : 403 (1909).

Plants 4·5–17·0 cm tall, light green, soft and gelatinous in texture. Main axes distinct, to 800 μm diam. below, gradually tapering to 220 μm diam. near the apex, naked at and near the base but elsewhere clothed with many branches of limited growth. These first-order branches 90–140 μm diam., closely surrounded by the peripheral branches 15–20 μm diam.

Floating off Cocos Bay with north-going currents.

Cocos Bay, 24 Mar. 1957, *Richardson 45*.

From Bermuda to Barbados.

14. *TRICHOSOLEN* Mont.

TRICHOSOLEN Mont. in Annls Sci. nat., ser. 4, Bot. 14 : 171 (1860).

1. ***Trichosolen duchassaingii*** (J. Ag.) W. R. Tayl. in Brittonia 14 : 62 (Jan. 1962) ; in Phycologia 2 : 26 (May 1962). (Plate 17 figs. 4–5.)

Bryopsis duchassaingii J. Ag. in Ofvers. K. VetenskAkad. Förh. Stockh. 11 : 107 (1854).
Trichosolen antillarum Mont. in Annls Sci. nat., ser. 4, Bot. 14 : 171 (1860).

Erect, dichotomously branched plants to 18 cm tall, main branches 650–1100 μm diam. and bearing many hair-like peripheral branches 1·0–2·0 mm long and 20–60 μm diam. The presence of gametangia on some branches readily distinguishes this genus from *Bryopsis*. In the Trinidad material the fertile branches each bear a single gametangium. Gametangia short-stalked (to 12 μm long), 75–225 μm long and 40–100 μm diam.

The nomenclature of this species has been considered by Taylor (1962b, c).

Rare in Trinidad, found only on three occasions as follows : a single plant in a eulittoral rock pool ; a small group of plants under a rock ledge in the upper sublittoral ; a number of individual plants floating with north-going currents off the east coast.

Maracas Bay, 19 May 1962, *Richardson 1134*. Saline Bay, 27 Mar. 1959, *Richardson 396*. Cocos Bay, 24 Mar. 1957, *Richardson 44*.

From Florida to Trinidad.

CAULERPACEAE

15. *CAULERPA* Lamour.

CAULERPA Lamour. in J. Bot. Paris 2 : 141 (1809).

KEY TO SPECIES

Plants without distinct stoloniferous and erect portions or, if distinct, of similar form . . . . 1. *C. fastigiata*
Plants with stoloniferous and erect portions which differ morphologically :
Branches or lobes of erect fronds each terminated by a short point :
Branching system verticillate . . . . . . 2. *C. verticillata*
Branching system simple with only occasional forking :
Peripheral branches compressed . . . . . . 3. *C. taxifolia*
Peripheral branches terete . . . . . . 4. *C. sertularioides*
Branches or lobes of erect fronds with smooth, rounded or flattened tips :
Peripheral branches subsessile, the very short stalk constricted at its apex 7. *C. microphysa*
Peripheral branches with a more obvious stalk not constricted at its apex :
Ends of peripheral branches terminating abruptly in a peltate disc 6. *C. peltata*
Ends of peripheral branches swollen, cylindrical, clavate to subspherical in shape, very variable . . . . 5. *C. racemosa*

1. ***Caulerpa fastigiata*** Mont. in Ramon de la Sagra, Hist. Phys. Polit. & Nat. Cuba, Bot., Pl. Cell. : 19 (1842).

Individual plants 2(–4) cm in length. Erect branches 80–150 μm diam. similar in form to stoloniferous branches, which are to 200 μm diam. Rhizoids freely branched, 25–75 μm diam.

In thick mats on rocks and mud, from the lower eulittoral to the upper sublittoral.

Saline Bay, 1 July 1957, *Richardson 83* ; 24 Apr. 1959, *Richardson 387*. Point Radix, 18 July 1957, *Richardson 122*. Taparo Point, July 1961, *Richardson 1088*. Scotland Bay, 24 Sept. 1957, *Richardson 224*. Perriquier Bay, 9 Mar. 1958, *Richardson 296*.

Bermuda to Panama, Brazil.

2. ***Caulerpa verticillata*** J. Ag. in Ofvers. K. VetenskAkad. Förh. Stockh. 4 : 6 (1847).

Branching verticillate, filiform branches 15–25 μm diam. near their tips, some to 2 cm long. Dense rhizoids grow from the horizontal branches.

Forming dark green carpets, completely covering some rocks, but other algae often grow up through the carpet, upper sublittoral.

Carenage, 5 Apr. 1958, *Richardson 315*.

From Bermuda to Brazil.

3. **Caulerpa taxifolia** (Vahl) Ag., Sp. Alg. 1 : 435 (1822).

Fucus taxifolius Vahl in Skr. Naturh.-Selsk. Kiobenhavn 5 (2) : 36 (1802).
Caulerpa taxifolia [var.] β *crassifolia* Ag., tom. cit. : 436 (1822).
Caulerpa mexicana Sond. ex Kütz., Sp. Alg. : 496 (1849).
Caulerpa crassifolia (Ag.) J. Ag. in Acta Univ. lund. 9 (8) : 13 (1873).

Well-developed fronds reach 13 cm in length and 1·5 cm in width. A few fronds branch. Peripheral branches 2–5 mm long and 0·5–1·0 mm wide, curving upwards slightly, terminated abruptly with a short point.

Scattered individuals creep over sandy and muddy rocks and stones at depths of 0·5–2·0 m.

Balandra Bay, Feb. 1957, *Richardson 57*. Saline Bay, 27 Feb. 1959, *Richardson 357, 357a*. Point Radix, 9 Mar. 1962, *Richardson 1131*. Taparo Point, July 1961, *Richardson 1115*.

From Bermuda to Brazil.

4. **Caulerpa sertularioides** (Gmel.) Howe in Bull. Torrey bot. Club 32 : 576 (1905).

Fucus sertularioides Gmel., Hist. Fuc. : 151 (1768).

Erect axes 2·0–7·5 cm tall and 12 mm wide, peripheral branches 4–8 mm long, terete. A few erect main axes branch but this is not common.

In sheltered localities, on small rocks and stones, or embedded in mud, from the upper sublittoral down to about 0·5 m.

Carenage, 3 Apr. 1958, *Richardson 314* ; 17 Feb. 1960, *Richardson 478*. Scotland Bay, 24 Sept. 1957, *Richardson 219, 227*. Perruquier Bay, 9 Mar. 1958, *Richardson 288*. Caledonia, 1893, *Hart*, Herb. Trin. no. 5469. Unknown locality, 1953, *Bedell 17*. Also recorded by Taylor (1960).

From Bermuda to Brazil.

5. **Caulerpa racemosa** (Forssk.) J. Ag. in Acta Univ. lund. 9 (8) : 35 (1873).

Fucus racemosus Forssk., Fl. Aegypt.-Arab. : 191 (1775).

Grows to 9 cm tall and bears peripheral branches 2–5 mm long, with a subglobose or flattened tip 1·0–2·5 mm diam. and a stalk 1–4 mm long.

Variable species occupying eulittoral pools and growing along the upper sublittoral in sheltered bays.

5a. **Caulerpa racemosa** var. **racemosa**.

Matelot, 30 July 1967, *Richardson 179*. L'Ainse Nicolas, 23 Feb. 1960, *Richardson 482*. Saline Bay, 27 Feb. 1959, *Richardson 353* ; 5 Apr. 1961, *Richardson 1041*. Perruquier Bay, 9 Mar. 1958, *Richardson 289*. Unknown locality, 1953, *Bedell 7*. Also recorded by Taylor (1960).

5b. ***Caulerpa racemosa*** var. ***clavifera*** (Turn.) Weber van Bosse in Annls Jard. bot. Buitenz. 15 : 361 (1898).

Saline Bay, 27 Feb. 1959, *Richardson 353b.*

5c. ***Caulerpa racemosa*** var. ***laetevirens*** (Mont.) Weber van Bosse, tom. cit. : 366 (1898).

Perruquier Bay, 9 Mar. 1958, *Richardson 295.*
The species as a whole occurs from Bermuda to Brazil.

6. ***Caulerpa peltata*** Lamour. in J. Bot. Paris 2 : 145 (1809).

C. racemosa var. *peltata* (Lamour.) Eubank in Univ. Calif. Publs Bot. 18 : 421 (1946).

Most plants 1–2(–5) cm tall. Peltate peripheral branches stalked, terminating in cup-shaped or flattened discs, 2–4 mm diam.

From exposed headland, forming matted growth over rocks along the upper sublittoral.

Balandra Bay, Feb. 1957, *Richardson 51* ; 22 July 1959, *Richardson 459, 460.*
From Bermuda to Barbuda, Brazil.

7. ***Caulerpa microphysa*** (Weber van Bosse) Feldm. in Revue gén. Bot. 62 : 424 (1955).

Caulerpa racemosa var. *clavifera* f. *microphysa* Weber van Bosse in Annls Jard. bot. Buitenz. 15 : 361 (1898).

Fronds to 8 mm tall, bearing short-stalked, spherical peripheral branches 1–2 mm diam. Stalks clearly constricted near apex.

From shaded, damp situation beneath overhanging rock ledge in the lower eulittoral.

Matelot, 30 July 1957, *Richardson 185.*
From Bermuda to Venezuela.

CODIACEAE

16. ***BOODLEOPSIS*** A. & E. S. Gepp

BOODLEOPSIS A. &. E. S. Gepp in Siboga Exped. 62 : 64 (1911).

1. ***Boodleopsis pusilla*** (Collins) Tayl., Joly & Bernat. in Pap. Mich. Acad. Sci. 38 : 105 (1953).

Dichotomosiphon pusillus Collins in Tufts Coll. Stud. 2 : 431 (1909).

Matted filaments difficult to separate, colourless below but green above, where they reach 45 μm diam. Upper branches constricted at the base.

Forming dark green turf on shaded rock faces embedded in surface deposit of mud along littoral fringe.

Perruquier Bay, 9 Mar. 1958, *Richardson 291*.

From Bermuda to Guadeloupe, Brazil.

17. *HALIMEDA* Lamour.

HALIMEDA Lamour. in Nouv. Bull. Soc. philom. Paris 3 : 186 (1812).

1. ***Halimeda opuntia*** (L.) Lamour., Hist. Polyp. Corall. Flex. : 308 (1816).

Corallina opuntia L., Syst. Nat., ed. 10, 1 : 805 (1758).

Not recorded by the author. Description based on Taylor (1960).

Plants whitish-green, calcified, 10–25 cm tall, spreading to form large colonies attached at irregular points. Made up of flexible joints and calcified segments, branching in all planes with successive branches and successive segments often at right angles to each other. The segments trilobed, with three radiating ribs evident on their surface. Segments 7–20 mm wide, 4·5–12·0 mm long. Surface utricles (12–)20–50(–63) μm diam.

On rocks, gravel and sand, upper sublittoral.

Recorded by Taylor (1960).

From Florida to Brazil.

18. *CODIUM* Stackh.

CODIUM Stackh., Ner. Brit. : xvi (1797).

KEY TO SPECIES

Plants decumbent, branches anastomosing . . . . . . 1. *C. repens*
Plants erect, branches not anastomosing :
  Branches cylindrical, end walls of utricles 15–30 μm thick . 2. *C. isthmocladum*
  Branches flattened, at least at the forks, end walls of utricles 4–7 μm thick 3. *C. taylorii*

1. ***Codium repens*** Crouan frat. ex Vickers in Annls Sci. nat., ser. 9, Bot. 1 : 56 (1905). (Plate 18 fig. 6.)

Branches anastomosing, less than 2 cm long and 0·2 cm diam. Utricles 570–760 μm long by 100–245 μm diam., end walls about 5 μm thick. Gametangia 225–300 μm long by 55–85 μm diam. Filaments 30–40 μm diam.

Small creeping plant found under rock ledges from the eulittoral to the upper sublittoral.

Matelot, 30 July 1957, *Richardson 176*.

From Bermuda to Barbados, Brazil.

2. **Codium isthmocladum** Vickers in Annls Sci. nat., ser. 9, Bot. 1 : 57 (1905).

In 'typical' specimens the thalli cylindrical, about 14 cm long and 3–4 mm diam., the utricles 700–860 μm long by 200–315 μm diam., with end walls 15–30 μm thick. Gametangia 140–215 μm long by 55–115 μm diam., filaments 30–60 μm diam. A closely branched, tufted form (*Richardson 177*) had more slender utricles. A proliferous habit, rare in this species, was shown by two specimens (*Richardson 226, 231*) from the sheltered habitat at Scotland Bay. The utricles of these specimens were short and squat, but the gametangia were typical. The Carenage specimens (*Richardson 307*) had exceptionally long interdichotomies.

Variable in Trinidad, growing on rocks and stones from lower eulittoral to 5 m depth.

Matelot, 30 July 1957, *Richardson 177*. Point Radix, 9 Mar. 1962, *Richardson 1132*. St Joseph, 11 July 1957, *Richardson 111*. Taparo Point, July 1961, *Richardson 1097*. Diego Islands, 18 Apr. 1939, *Taylor 39-485* (Taylor, 1942). Carenage, 3 Apr. 1958, *Richardson 307* ; 17 Feb. 1960, *Richardson 473*. Scotland Bay, 24 Sept. 1957, *Richardson 226, 231*.

From Bermuda to Brazil.

3. **Codium taylorii** Silva in Nova Hedwigia 1 : 510 (1960), 'taylori'.

Plants 5–6 cm, short and stumpy with flattened sub-dichotomous to irregular branches. Utricles slender, 640–900 μm long by 185–430 μm diam., end walls 4–7 μm thick. Filaments 35–65 μm diam. ; no gametangia observed.

In shallow pools in the lower eulittoral.

Matelot, 30 July 1957, *Richardson 186*.

From Bermuda to Brazil.

PHAEOPHYCEAE

KEY TO GENERA

Plants filamentous :
- Filaments at least partly polysiphonous, the cells in polysiphonous parts arranged in tranverse rows . . . . 4. *Sphacelaria*
- Filaments entirely monosiphonous :
  - Chromatophores stellate, reproductive organs intercalary . 1. *Bachelotia*
  - Chromatophores discoid or linear, reproductive organs terminal or lateral on branches :
    - Chromatophores discoid . . . . 3. *Giffordia*
    - Chromatophores linear . . . . 2. *Ectocarpus*

Plants not filamentous :
- Plants with terete axes bearing distinct foliar organs, vesicles frequently present 13. *Sargassum*

- Plants thalloid, filiform or spherical, without distinct foliar organs or vesicles :
  - Plants thalloid with strap-shaped branches or fan-shaped foliaceous segments, growth from apical cells or marginal rows of apical cells :
    - Thallus with strap-shaped to foliaceous branches :
      - Branches with midribs . . . . 7. *Dictyopteris*
      - Branches without midribs :
        - Thallus branches less than 1 cm broad, each growing from a single conspicuous apical cell . . . . . 5. *Dictyota*
        - Thallus branches more than 1 cm broad, without a single conspicuous apical cell . . . . 6. *Spatoglossum*
    - Thallus entire or lobed or split, the segments essentially fan-shaped :
      - Apical margins of thallus inrolled . . . . . . 9. *Padina*
      - Apical margin of thallus not inrolled . . . . 8. *Lobophora*
  - Plants filiform or spherical and hollow, growth usually intercalary but sometimes apical :
    - Plants spherical . . . . 10. *Colpomenia*
    - Plants with elongate, simple or branched axes :
      - Axes and branches solid, often compressed . . 12. *Chnoospora*
      - Axes terete, hollow . . . . . . 11. *Rosenvingea*

ECTOCARPACEAE

1. ***BACHELOTIA*** (Bornet) Kuckuck ex Hamel

BACHELOTIA (Bornet) Kuckuck ex Hamel in Bot. Notiser 1939 : 66 (1939) ; Phéophyc. France : *X* (1939).

Pylaiella subgen. *Bachelotia* Bornet in Revue gén. Bot. 1 : 8 (1889).

1. ***Bachelotia antillarum*** (Grun.) Gerloff in Nova Hedwigia 1 : 37 (1959). (Plate 19 fig. 4.)

Ectocarpus antillarum Grun. in Fenzl, Reise Osterr. Fregatte Novara um die Erde, Bot. 1 : 46 (1868).
Pylaiella fulvescens Bornet in Revue gén. Bot. 1 : 8 (1889).
Pylaiella antillarum (Grun.) De Toni, Syll. Alg. 3 : 535 (1895).
Bachelotia fulvescens (Bornet) Kuckuck ex Hamel in Bot. Notiser 1939 : 66 (1939) ; Phéophyc. France : *XIII* (1939).

The cells of the filaments 25–40 μm broad and 25–110 μm long, being 1–2 times as long as broad. Each cell with one or two typical stellate chromatophores, as discussed by Blomquist (1958).

Light yellow-brown tufts, 2–5 cm high, on rock faces and loose stones in the upper eulittoral.

Othoe Point, 6 Feb. 1958, *Richardson 264*. Taparo Point, July 1961, *Richardson 1108*. Carenage, 3 Apr. 1958, *Richardson 309*. Perruquier Bay, 9 Mar. 1958, *Richardson 282*.

From Bermuda to Virgin Islands, Brazil.

2. *ECTOCARPUS* Lyngb.

Ectocarpus Lyngb., Tent. Hydrophyt. Dan. : 130 (1819), *nom. cons.*

1. ***Ectocarpus breviarticulatus*** J. Ag. in Ofvers. K. VetenskAkad. Förh. Stockh. 4 : 7 (1847). (Plate 19 figs. 2, 3, 6.)

Tufts consist of entangled, branched filaments, 20–30 μm diam., the cells being 2–4 times as long. Branch tips often hooked. Plurilocular sporangia ovoid, 30–50 μm by 30–40 μm, borne at right angles to the filament on short 1–2-celled stalks.

Forming small olive-brown ropy tufts, 2–4·5 cm tall, on small rocks along the upper sublittoral.

Maracas Bay, 19 May 1962, *Richardson 1135*.

From Jamaica to Brazil.

3. *GIFFORDIA* Batters

Giffordia Batters in Grevillea 21 : 86 (1893).

Key to Species

Plants to 2·5(–4·5) cm tall ; plurilocular sporangia, irregularly distributed on branches, usually 4–5 times their diameter in length . . 2. *G. indica*

Plants often more than 3(–8) cm tall but variable ; plurilocular sporangia, in rows on upper (adaxial) sides of branches, usually 2·5–4·5 times their diameter in length 1. *G. mitchelliae*

1. ***Giffordia mitchelliae*** (Harv.) Hamel, Phéophyc., France : *XIV* (1939).

Ectocarpus mitchelliae Harv. in Smithson. Contr. Knowl. 3 (4) : 142 (1851) '*Mitchellae*'.

Cells 15–35 μm diam. by 20–90 μm long, being (1–)1·5–3·5(–4) times as long as broad. Only few unilocular sporangia observed, 40 μm diam. by 70 μm long. Plurilocular sporangia 15–35 μm diam. by 50–135 μm long and 2·5–4·5 times as long as broad, in rows on adaxial side of branches.

Forming tufts (1–)3(–8) cm in length on rocks and loose stones from the eulittoral down to the upper sublittoral.

Saline Bay, 1 July 1957, *Richardson 84* ; 25 Nov. 1957, *Richardson 234*. Carenage, 17 Feb. 1960, *Richardson 479*. La Tinta Bay, 31 Jan. 1960, *Richardson 470*.

From Bermuda to Guadeloupe, Brazil.

2. ***Giffordia indica*** (Sonder) Papenf. & Chih. apud Papenf. in Israel J. Bot. 17 : 30 (1968).

Ectocarpus indicus Sonder in Zoll., Syst. Verz. Ind. Archipel. 1842–48 empf. Pfl. 1 : 3 (1854).
Ectocarpus duchassaingianus Grun. in Fenzl, Reise Osterr. Fregatte Novara um die Erde, Bot. 1 : 45 (1868).
Giffordia duchassaingiana (Grun.) W. R. Tayl., Mar. Alg. E. Trop. & Subtrop. Coasts Amer. : 207 (1960).
Feldmannia indica (Sonder) Womersl. & Bail. in Phil. Trans. R. Soc., B, 259 : 288 (1970).

Tufts 2·5(–4·5) cm tall. Main filamentous axes 20–30 μm diam., branches taper to 10 μm near apex. Cells 30–90 μm long, being 1–3 times their diameter. Plurilocular sporangia 30–50 μm diam. and 115–220 μm long, 4–5 times as long as their diameter, rounded at the apex, uneven in outline and sessile ; irregularly distributed on the branches. Loculi 5–7 μm high.

Womersley & Bailey (1970) discuss evidence for placing this species in the genus *Feldmannia.*

On small rocks in light brown to yellow-brown tufts along the lower eulittoral and the upper sublittoral.

Balandra Bay, 22 July 1959, *Richardson 430.*

From Bermuda to Tobago.

SPHACELARIACEAE

4. *SPHACELARIA* Lyngb.

SPHACELARIA Lyngb., Tent. Hydrophyt. Dan. : 103 (1819).

1. ***Sphacelaria tribuloides*** Menegh., Lett. Prof. G. Menegh. al Dott. J. Corinaldi a Pisa 1 : 2 (23 May 1840) ; in Flora 23 : 512 (28 Aug. 1840). (Plate 19 fig. 5.)

Forming dark brown to black tufts 1–1·5 cm tall. Filaments 40 μm diam., formed of two cell layers except at the tips where the terminal, single row of cells is sometimes swollen. Propagules triangular.

On tops of rocks along upper sublittoral together with *Enteromorpha* sp. and *Giffordia mitchelliae.*

Saline Bay, 26 May 1959, *Richardson 403.*

From Bermuda to Brazil.

DICTYOTACEAE

5. *DICTYOTA* Lamour.

DICTYOTA Lamour. in J. Bot. Paris 2 : 38 (Apr. 1809) ; in Nouv. Bull. Soc. philom. Paris 1 : 331 (May 1809), *nom. cons.*

Key to Species

Branching pattern towards the apices alternate . . . . . 5. *D. dentata*

Branching pattern towards the apices dichotomous or cervicorn :

  Thallus margin dentate . . . . 4. *D. ciliolata*

  Thallus margin entire :

    Branching of mature plants cervicorn or irregular . . 3. *D. cervicornis*

    Branching of the mature plants essentially dichotomous :

      Young branch tips filiform, less than 0·5 mm broad, often with sharp transition between old and young thallus . . . 2. *D. divaricata*

      Branch tips not filiform, more than 1 mm broad, no sharp transition from young to old thallus . . . . . . 1. *D. dichotoma*

1. ***Dictyota dichotoma*** (Huds.) Lamour. in J. Bot. Paris 2 : 42 (Apr. 1809) ; in Nouv. Bull. Soc. philom. Paris 1 : 331 (May 1809). (Plate 20 fig. 1.)

Ulva dichotoma Huds., Fl. Angl. : 476 (1762).

Thallus to 12 cm tall and 4–7 mm broad below the dichotomies, 2–4 mm above. Tetrasporangia scattered, 90–115 μm diam. Antheridia 10–20 μm diam., to 50 μm tall, grouped in sori of 100–200 μm diam.

Shallow water plant to depth of about 0·5 m.

Carenage, 3 Apr. 1958, *Richardson 319* ; 17 Feb. 1960, *Richardson 476*. Perruquier Bay, 9 Mar. 1958, *Richardson 286*. South Side, Chacachacare, 12 Apr. 1961, *Richardson 1048*. Gasparee, Apr. 1895, *Hart 5803*.

From Bermuda to Brazil.

2. ***Dictyota divaricata*** Lamour. in J. Bot. Paris 2 : 43 (Apr. 1809) ; in Nouv. Bull. Soc. philom. Paris 1 : 331 (May 1809).

Less than 7 cm long, very entangled, prostrate and clearly dichotomously branched. Abrupt change from relatively wide old thallus, 1–4 mm broad below the forks, to filiform young branch tips about 0·2 mm broad. Angle of branching generally 45–90°, rather less than found by Taylor (1960), 90–120°. Branches sometimes spirally twisted or bearing many proliferations. In transverse section thallus to 320 μm thick. Tetrasporangia (*Richardson 414* from Saline Bay) 115–145 μm diam. by 70 μm high. Antheridial sori 55–240 μm diam., the antheridia 14–15 μm diam.

Common on stones, rocks and sometimes epiphytic on other algae, from lower eulittoral down to depth of 2–5 m.

Balandra Bay, 22 July 1959, *Richardson 377*. Saline Bay, 24 Apr. 1959, *Richardson 372* ; 7 July 1959, *Richardson 413, 414*. Taparo Point, July 1961, *Richardson 1116* ; Diego Islands, 18 Apr. 1939, *Taylor 39-488* (Taylor, 1942). St Pierre, 3 Apr. 1958, *Richardson 325*. Carenage, 17 Feb. 1960, *Richardson 476*. Scotland Bay, 24 Sept. 1957, *Richardson 209, 218*.

From Bermuda to Brazil.

3. ***Dictyota cervicornis*** Kütz., Tab. Phyc. 9 : 11 (1859). (Plate 20 fig. 2.)

Thallus 6–8 cm tall, 1–2 mm broad immediately above the dichotomies and 2–4 mm below the dichotomies. Branching dichotomous to cervicorn. Thallus 120–140 μm thick, bearing tetrasporangia and a few antheridia on both surfaces. Tetrasporangia 65–130 μm diam. 75–110 μm high. Antheridia 10–15 μm diam. 40–45 μm high, grouped in sori, 75–95 μm diam.

Plant in small clumps, scattered along upper sublittoral and down to depth of about 0·5 m.

The specimen from Perruquier Bay (*Richardson 287*) was often growing alongside *Dictyota dichotoma* and appeared distinctly different under natural conditions, being much darker. This difference is much less obvious in dried specimens. Unless cervicorn branching is present these two species may prove difficult to distinguish.

Scotland Bay, 24 Sept. 1957, *Richardson 208*. Perruquier Bay, 9 Mar. 1958, *Richardson 287*.

From Bermuda to Brazil.

4. **Dictyota ciliolata** Kütz., Tab. Phyc. 9 : 12 (1859). (Plate 20 fig. 3.)

Plants from Maqueripe Bay less than 3 cm forming a sward on seaward faces of rocks along upper sublittoral. Other specimens completely submerged or awash, length to 12–14 cm, the branches to 4–5 mm in width. All specimens with dentate margins, branching dichotomously at an angle between 30° and 60°, the branches often twisted. Thallus 80–140 μm thick. Tetrasporangia 45–100 μm diam., borne on both surfaces of thallus.

Sublittoral species down to 1 m depth and recorded mainly from the north and north-east coasts of Trinidad.

Maqueripe Bay, 15 Aug. 1957, *Richardson 198*. Chupara Bay, 17 June 1957, *Richardson 74*. Matelot, 30 July 1957, *Richardson 160*. Balandra Bay, Feb. 1957, *Richardson 49* ; 22 July 1959, *Richardson 399*. Saline Bay, 27 Mar. 1959, *Richardson 382* ; 7 July 1959, *Richardson 409*. La Tinta Bay, 20 Jan. 1957, *Richardson 32* ; 31 Jan. 1960, *Richardson 467*.

From Bermuda to Brazil.

5. **Dictyota mertensii** (Mart.) Kütz., Tab. Phyc. 9 : 15, t. 36 fig. I (1859).

Fucus atomarius Gmel., Hist. Fuc. : 125 (1768), non *Dictyota atomaria* (Woodw.) Grev. (1830).

Dictyota dentata Lamour. in J. Bot. Paris 2 : 42 (Apr. 1809) ; in Nouv. Bull. Soc. philom. Paris 1 : 331 (May 1809), *nom. superfl.*

Ulva mertensii Mart., Ic. Select. Pl. Crypt. Brasil. : 5, t. 1 (1828).

Dictyota brongniartii J. Ag. in Linnaea 15 : 5 (1841).

Not recorded by author. Description based on Taylor (1960, as *D. dentata*).

Plants bushy, 10–20 cm tall, the main axes to 6 mm broad, bearing alternate lateral branches at intervals of 1–2 cm. Peripheral branches spur-like, 1–2 mm long, branch tips rounded on young shoots, becoming dentate.

On rocks from lower eulittoral to sublittoral especially at about 2 m depth.

Lamouroux stated that his *Dictyota dentata* was founded on *Fucus atomarius* Gmel., and hence his name is superfluous and illegitimate. The combination *Dictyota atomaria* based on *Fucus atomarius* cannot now be made because of *Dictyota atomaria* (Woodw.) Grev., based on *Ulva atomaria* Woodw. (*Taonia atomaria* (Woodw.) J. Ag.). Hence *Ulva mertensii* Mart. provides the first available legitimate epithet for this species.

Unknown locality, Apr. 1912–May 1913, Thaxter (Taylor, 1929).

From Bermuda to Brazil.

6. *SPATOGLOSSUM* Kütz.

SPATOGLOSSUM Kütz., Phyc. Gen. : 339 (1843).

1. **Spatoglossum schroederi** (Ag.) Kütz., Tab. Phyc. 9 : 21 (1859).

Zonaria schroederi Ag., Syst. Alg. : 265 (1824).

Iridescent fronds to 35 cm tall, branches to 2(–5) cm broad. Margins of frond often dentate, proliferating readily. Tetrasporangia to 110 μm diam., on both surfaces of fronds. Few antheridial sori, the antheridia 15 μm diam.

Sublittoral below 0·5 m depth.

Balandra Bay, 9 Jan. 1949, *Senior White*, cast; 15 Mar. 1959, *Richardson 361*. Saline Bay, 27 Feb. 1959, *Richardson 350*. St Joseph, 11 July 1957, *Richardson 110*, cast. Taparo Point, July 1961, *Richardson 1100*.

From Bermuda to Brazil.

7. ***DICTYOPTERIS*** Lamour.

DICTYOPTERIS Lamour. in Nouv. Bull. Soc. philom. Paris 1 : 332 (1809), *nom. cons.*

KEY TO SPECIES

Lamina dark, firm, 4 cells thick, more than 1·5 cm broad . . 1. *D. justii*
Lamina almost transparent, pliable, 2 cells thick, less than 0·5 cm broad 2. *D. delicatula*

1. ***Dictyopteris justii*** Lamour. in Nouv. Bull. Soc. philom. Paris 1 : 332 (1809).

Not recorded by author. Description based on Taylor (1960).

Plants to 40 cm tall, dark brown. Branching dichotomous, the strap-shaped branches sometimes ruffled, 1·5–8·0 cm broad at the tips. Midrib prominent, forming basal stipe after old lamina disintegrates. Groups of hairs scattered over the lamina, the fertile sori in large patches on upper parts of lamina.

On eulittoral rocks but also in sublittoral.

Unknown locality, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929).

From Bermuda to Brazil.

2. ***Dictyopteris delicatula*** Lamour. in Nouv. Bull. Soc. philom. Paris 1 : 332 (1809).

Length to 7 cm but Maqueripe Bay specimens less than 2 cm. Fronds dichotomously branched, with prominent midrib, to 3 mm broad. Matelot plants mainly upright, but other collections prostrate, often entangled, with few or no upright parts to thallus. In section the thallus two celled and 70–150 μm thick.

Forming dense mats on rock faces or mixed with other matted algae of the upper sublittoral and down to depth of about 1·5 m.

Maqueripe Bay, 15 Aug. 1957, *Richardson 199*. Maracas Bay, 22 July 1956, *Richardson 5*, cast. Matelot, 30 July 1957, *Richardson 174*. Balandra Bay, 9 Jan. 1949, *Senior White*, cast; 22 July 1959, *Richardson 435, 446*. Saline Bay, 26 May 1959, *Richardson 408*. Unknown locality, 1953, *Bedell 2*; Apr. 1912–May 1913, *Thaxter* (Taylor, 1929, as *Neurocarpus delicatulus*).

From Bermuda to Brazil.

8. ***LOBOPHORA*** J. Ag.

LOBOPHORA J. Ag. in Acta Univ. lund. 29 : 21 (1894).

1. ***Lobophora variegata*** (Lamour.) Womersl. in Aust. J. Bot. 15 : 221 (1967). (Plate 19 fig. 7.)

Dictyota variegata Lamour. in J. Bot. Paris 2 : 40 (Apr. 1809) ; in Nouv. Bull. Soc. philom. Paris 1 : 331 (May 1809).
Zonaria variegata (Lamour.) Mart., Ic. Select. Pl. Crypt. Brasil. : 6, t. 2 fig. 2 (1828).
Lobophora nigrescens J. Ag. in Acta Univ. lund. 29 : 23 (1894).
Pocockiella variegata (Lamour.) Papenf. in Am. J. Bot. 30 : 467 (1943).

Thallus light brown, in part prostrate, to 5 cm long, at least half the length of the thallus turning upwards, the lobes reaching 4 cm in width. In transverse section the central medulla cells 30 × 90 μm, the cortex cells 15 μm wide by 25–90 μm long. Sporangia in sori on both surfaces of the thallus, and, when young, covered by a thin membrane. Mature sporangia 70 μm diam., 85 μm tall. Hairs present but infrequent.

At depth of about 1 m at Saline Bay and at base of a large boulder in the upper sublittoral at Balandra Bay.

Balandra Bay, 22 July 1959, *Richardson 440*. Saline Bay, 24 Apr. 1959, *Richardson 373*.

From Bermuda to Barbados, Brazil.

9. *PADINA* Adans.

PADINA Adans., Fam. Pl. 2 : 13, 586 (1763), *nom. cons.*

KEY TO SPECIES

Developing sporangia covered by membrane and arranged in one or two often rather indistinct bands	1. *P. vickersiae*
Developing sporangia without membrane and arranged as single bands each between a pair of distinctive hair bands	2. *P. gymnospora*

1. ***Padina vickersiae*** Hoyt apud Howe in Britton & Millsp., Bahama Fl. : 595 (26 June 1920) ; in Bull. Bur. Fish., Wash. 36 : 456 (30 Dec. 1920). (Plate 19 fig. 8.)

Thalli range from 2–14 cm in height, fan out to maximum width of 18 cm. Smaller plants consist of leathery holdfast, very short stipe and single, lobed, fan-shaped frond. In larger plants the frond may be split into as many as nine ragged lobes, naked below. Hair bands often poorly developed, but when clear 1–6 mm apart. Fronds 40–140 μm thick, composed of four to six cell layers. Sporangia 70–100 μm diam., covered by membrane until mature, forming one or two bands between the hair bands, on both surfaces of frond. Oogonia (*Richardson 30* from La Tinta Bay) 40–55 μm diam., 70–80 μm tall.

On rocks along upper sublittoral, frequently embedded in sand. Trinidad specimens variable.

Matelot, 30 July 1957, *Richardson 155*. Balandra Bay, 15 Mar. 1959, *Richardson 365*. Saline Bay, 27 Feb. 1959, *Richardson 355* ; 24 Apr. 1959, *Richardson 380*. Soldado Rock, 30 Apr. 1961, *Richardson 1054*. Carenage, 3 Apr. 1958, *Richardson 316*. La Tinta Bay, 20 Jan. 1957, *Richardson 30*. Caledonia, 1893, *Hart 5471*. Islands, May 1914, *McLean*.

From Bermuda to Brazil.

2. **Padina gymnospora** (Kütz.) Vickers in Annls Sci. nat., sér. 9, Bot. 1 : 58 (1905). (Plate 20 fig. 4.)

Zonaria gymnospora Kütz., Tab. Phyc. 9 : 29 (1859).

Plants 8–10(–12) cm tall, and to 15 cm broad. Thallus two cell layers thick, about 60 μm near the tip, but three cell layers thick and about 100 μm in older parts. Hair bands 1–2·5 mm apart, a pair of hair bands enclosing each band of sporangia. The sporangia 85–95 μm diam., in groups, but without covering membrane. Bands of sporangia near the tips with tetraspores but the older bands usually empty.

Extends from upper sublittoral to about 1 m depth.

Carenage, 17 Feb. 1960, *Richardson 474*. Chacachacare, South Side, 12 Apr. 1961, *Richardson 1045*. Also recorded by Taylor (1960).

From Bermuda to Brazil.

PUNCTARIACEAE

10. COLPOMENIA Derb. & Solier

COLPOMENIA Derb. & Solier in Suppl. C. r. hebd. Séanc. Acad. Sci., Paris 1 : 11 (1856).

1. **Colpomenia sinuosa** (Roth) Derb. & Solier in Suppl. C. r. hebd. Séanc. Acad. Sci., Paris 1 : 11 (1856).

Ulva sinuosa Roth, Cat. Bot. 3 : 327 (1806).

Light brown ; undamaged plants spherical, 3 cm diam. Wall in thickest parts 500 μm. Surface cells 11–14 μm diam., internal cells 140 μm diam., colourless. Paraphyses 11 μm diam., 80 μm long.

Few plants in cast at Guayaguayare Bay.

Guayaguayare Bay, 14 March 1960, *Richardson 1009*.

From Bermuda to Brazil.

11. ROSENVINGEA Børg.

ROSENVINGEA Børg. in Dansk bot. Ark. 2 (2) : 22 (1914), reimpr. ut Mar. Alg. Danish W. Indies : 178 (1914).

1. **Rosenvingea intricata** (J. Ag.) Børg. in Dansk bot. Ark. 2 (2) : 26 (1914), reimpr. ut Mar. Alg. Danish W. Indies : 182 (1914).

Asperococcus intricatus J. Ag. in Ofvers. K. VetenskAkad. Förh. Stockh. 4 : 7 (1847).

Plants to 6 cm tall, the main axes to 8 mm diam., terete and hollow, narrowing sharply to branch tips which are 0·2 mm diam.

Few isolated plants growing on small stones in shallow water at head of sheltered bay, also dredged at 2–5 m depth.

Diego Islands, 18 Apr. 1939, *Taylor 39-489* (Taylor, 1942). Scotland Bay, 24 Sept. 1957, *Richardson 220*.

From Bermuda to Brazil.

12. ***CHNOOSPORA*** J. Ag.

CHNOOSPORA J. Ag. in Ofvers K. VetenskAkad. Förh. Stockh. 4 : 7 (1847).

1. ***Chnoospora minima*** (Hering) Papenf. in Jl S. Afr. Bot. 22 : 69 (1956).

Fucus minimus Hering in Ann. Mag. nat. Hist. 8 : 92 (1841).

Thallus erect, to about 5 cm tall, branching irregularly dichotomous, sometimes with many proliferous branches. Thallus branches solid, flattened, 2–3 mm broad, broadest just below the forks. Covered with hairs 13–15 μm diam. and 80 μm long.

On sublittoral rocks at depth of about 0·5 m.

L'Ainse Nicolas, 12 Aug. 1956, *Richardson 24*.

From Guadeloupe to Brazil.

SARGASSACEAE

13. ***SARGASSUM*** Ag.

SARGASSUM Ag., Sp. Alg. 1 : 1 (1820), *nom. cons.*

KEY TO SPECIES

'Leaves' mostly lanceolate to linear, 7–50 times as long as broad :
'Leaves' pliable, margins serrate . . . . . . 1. *S. filipendula*
'Leaves' firm, margins entire :
'Leaves' terete or scarcely flattened, mostly 1–2 mm diam. 5. *S. desfontainesii*
'Leaves' flattened, mostly more than 2 mm in diam. . . 3. *S. cymosum*
'Leaves' from narrowly oblong or lanceolate to ovate, less than 9 times as long as broad :
Receptacles palmated with subterete or flattened lobes . . 4. *S. hystrix*
Receptacles not palmated or flattened . . . . . . 2. *S. vulgare*

1. ***Sargassum filipendula*** Ag., Syst. Alg. : 300 (1824).

Dominant main branches smooth, 35–45 cm long, bearing many side branches 5–6 cm long. 'Leaves', vesicles and receptacles develop on side branches. Mature 'leaves', 17–40 mm long by 1–4 mm broad (8–20 times as long as broad), often forked, with serrate margins and a central midrib. 'Leaf' surfaces covered by numerous cryptostomata, 85–145 μm diam. Vesicles spherical, 4 mm diam., a few with a small terminal appendage, the vesicle stalks 3–4 mm. Receptacles elongated and branched.

From sheltered waters at depth of 0·5 m or less, attached to rocks and stones.

Carenage, 3 Apr. 1958, *Richardson 308*. Perruquier Bay, 9 Mar. 1958, *Richardson 285*. Unknown locality, 1952–3, *Bedell.*

From Bermuda to Brazil.

2. ***Sargassum vulgare*** Ag., Sp. Alg. 1 : 3 (1820).

Trinidad specimens range up to large robust plants, some 70 cm long but most 30–50 cm. 'Leaves' with central midrib, acutely serrate along their margins. Small cryptostomata, 70–145 μm diam., irregularly scattered over the 'leaf' surface. Mature 'leaves' lanceolate, 3–9(–10) times as long as broad, (11–)20–40 mm long and 3–10 mm broad. Vesicles usually present, spherical to ovoid, 3–5 mm diam., some showing a terminal foliose appendage or a foliose stalk or both. Receptacles irregularly branched, some elongate, others short and stubby.

From upper sublittoral and sublittoral down to depth of 3 m, growing vigorously under conditions of good aeration and moderate exposure. Some extensive beds were located in the Saline Bay area.

Saline Bay, 1 July 1957, *Richardson 85* ; 25 Nov. 1957, *Richardson 235* ; 27 Feb. 1959, *Richardson 340*. Taparo Point, July 1961, *Richardson 1090*. Soldado Rock, 30 Apr. 1961, *Richardson 1052*.

From Bermuda to Brazil.

3. ***Sargassum cymosum*** Ag., Sp. Alg. 1 : 20 (1820).

Not recorded by author. Description based on Taylor (1942, 1960).

Plants dark brown, often glaucous when dried. Elongate axes slender, smooth ; 'leaves' elliptical to linear usually more than 2 mm broad but narrow in relation to length. Vesicles few, spherical, often mucronate. Fertile branches about half as long as subtending 'leaves', repeatedly dichotomously branched.

Sublittoral, 2–5 m depth.

Diego Islands, 18 Apr. 1939, *Taylor 39–487* (Taylor, 1942).

From Bermuda to Brazil.

4. ***Sargassum hystrix*** J. Ag. in Ofvers. K. VetenskAkad. Förh. Stockh. 4 : 7 (1847).

Thallus 20–30 cm long, the 'leaves' acutely serrated along their margins, with a central midrib and small, scattered cryptostomata 100–140 μm diam. Most mature 'leaves' are 2–4 times as long as broad, 15–30 mm long × 5–15 mm broad. Vesicles infrequent, ovoid, 3–4 mm × 5–6 mm, with a short stalk 3 mm long. Both foliose stalk and terminal appendage occasionally observed.

Along upper sublittoral and down to depth of 0·5 m.

Balandra Bay, 25 Nov. 1957, *Richardson 244* ; 22 July 1959, *Richardson 393* ; 13 Sept. 1961, *Richardson 1118*. Also recorded by Taylor (1960).

From Bermuda to Brazil.

5. ***Sargassum desfontainesii*** (Turn.) Ag., Sp. Alg. 1 : 25 (1820). (Plate 20 figs. 5–7.)

Fucus desfontainesii Turn., Fuci 3 : 130 (1811).

Plants to about 27 cm in length, attached by a discoid or rather irregularly shaped holdfast. The stipe short, to 2·5 cm long, and very much reduced in some plants. Several branches arise from stipe (5–7) and may reach 25 cm in length, the lower and outer branches being the shortest and the upper and inner branches the longest. These main branches bear many, alternate, finely divided 'leaves' or branches of 7·5 cm length, and 1·5–2(–4) mm width. In broader, flattened branches a midrib is discernible. All parts of plants have cryptostomata, 125–200 μm × 90–125 μm, irregularly scattered over the branches and vesicles. A few vesicles stalked, 3–4 mm, spherical or slightly longer than broad, 3–4 mm. One beaked vesicle observed.

Receptacular branches on side branches from the main axes, terete, to 2 cm long, bearing branched receptacles to 1 cm long and to 640 μm in diameter. Most conceptacles male, the antheridia being 43–54 μm × 13–19 μm. Sterile hairs, 10 μm diam., containing plastids, and with cells 7 times as long as the diameter. Each female conceptacle with four oospheres which are 180 μm diam. and at maturity lie outside the conceptacle ensheathed in colourless mucilage.

From shallow depths, 0·5 m, off the south coast of Chacachacare. A pure stand of this species covers a considerable area.

The determination of this specimen is tentative. It agrees quite well with Turner's original description of *Fucus desfontainesii* from the Canary Isles. It has also been noted that Grunow (1916) records *Sargassum desfontainesii* (Turn.) J. Ag. 'ad insulam Trinidad (Herb. Sonder)'.

Chacachacare, South Side, 12 Apr. 1961. *Richardson 1044.*

Taylor (1960) lists this species under 'Uncertain Records' giving locality as Guadeloupe. The Trinidad material is described here fully since there is no recent published information on the species.

RHODOPHYCEAE

KEY TO GENERA

Thallus calcareous :
  Thallus crustose . . . . 10. *Lithophyllum*
  Thallus not crustose but built up of erect articulated axes and branches :
    Erect axes lightly to moderately calcified throughout, the articulations not flexible, not arising from crustose basal disc . . 3. *Galaxaura*
    Erect axes composed of alternating calcified segments and flexible articulations, arising from crustose basal discs :
      Branching pinnate ; conceptacles marginal or terminal 12. *Corallina*
      Branching dichotomous or irregular ; conceptacles scattered over the surface of the segments . . . . . . 11. *Amphiroa*
Thallus not calcareous :
  Thallus crustose, consisting of epiphytic discs formed by decumbent radial filaments . . . . 1. *Erythrocladia*

Thallus not crustose :
Thallus filamentous, at least younger parts showing monosiphonous structure :
Filaments unbranched, monosiphonous at first but becoming strap-shaped 2. *Erythrotrichia*
Filaments branched :
Filamentous axes monosiphonous throughout or sometimes with a few irregular corticating filaments growing from the nodes over the main axes . . . . 24. *Wrangelia*
Filamentous axes monosiphonous in early development but the main axes becoming polysiphonous, or the monosiphonous axes becoming ± completely obscured by cortication :
Axes polysiphonous (central filament of cells, each cell surrounded by pericentral cells of equal length), sometimes corticate :
Ultimate peripheral branches monosiphonous at least at the tips :
Branches arranged radially, branch tips not incurved 33. *Murrayella*
Branches arranged in two rows, the branch tips often incurved 34. *Bostrychia*
Ultimate peripheral branches polysiphonous :
Axes closely invested with distinctive short branches 31. *Bryocladia*
Axes not invested with short branches . . 30. *Polysiphonia*
Axes remaining monosiphonous but becoming partially or completely covered with corticating cells which are distributed less regularly than pericentral cells :
Cortication continuous in main axes but only at nodes in ultimate peripheral branches. . . . . 28. *Spyridia*
Cortication similar throughout branches of all orders :
Nodes with whorls of spines . . . 27. *Centroceras*
Nodes without whorls of spines :
Thallus creeping, branching pinnate, the branches flattened ; cortication complete . . . 26. *Reinboldiella*
Thallus erect, branching not pinnate, the branches terete but the basal portion may consist of creeping terete filaments ; cortication at the nodes only . . 25. *Ceramium*
Thallus cylindrical, compressed or membranous, no evident monosiphonous structure even in younger parts :
Thallus terete or somewhat flattened, less than 1 cm broad ; tips of branches not inrolled :
Thallus branches constricted into ovoid segments with no midrib ; plants usually less than 2 cm tall . . . . 19. *Catenella*
Thallus branches not constricted into ovoid segments, or if so constricted the segments with distinct midrib ; plants usually more than 2 cm tall :
Thallus consisting of a strong slender stem-like system bearing vesicular branches . . . . . . 22. *Botryocladia*

Thallus without vesicular branches :
Plants with one central axial filament :
Ultimate branches clearly polysiphonous, plants somewhat fleshy :
Apical cells sunk in pits at the tips of the branches 38. *Laurencia*
Apical cells not sunk in pits :
Axes compressed, branching pinnate 32. *Bryothamnion*
Axes terete, branching radial 37. *Acanthophora*
Ultimate branches not polysiphonous :
Branches with evident midrib 29. *Caloglossa*
Branches without midrib :
Branch tips often hooked or curved, branches not notably wide angled 20. *Hypnea*
Branch tips not hooked, branches wide angled 8. *Endocladia*
Plants with more than one central axial filament :
Plants with two central axial filaments (Pl. 24 fig. 6) 9. *Ochtodes*
Plants with three or more central axial filaments :
Plants gelatinous or fleshy in texture :
Medulla parenchymatous, cortex of small assimilative cells 17. *Gracilaria*
Medulla of anastomosing filaments, cortex of branched filaments loosely arranged in the inner part of cortex, compact in outer part :
Plants gelatinous, thallus terete except for slight flattening below branch axils ; medulla with conspicuous stellate 'ganglia' (Pl. 24 fig. 5) 13. *Halymenia*
Plants fleshy to cartilaginous, thallus terete and radially branched or flat and pinnately branched, medulla without stellate 'ganglia' 14. *Grateloupia*
Plants wiry or tough in texture :
Rhizines present at least in older parts of the plant :
Rhizines mainly in central medulla (Pl. 24 fig. 1) 7. *Pterocladia*
Rhizines mainly in sub-cortical regions (Pl. 24 fig. 2) 6. *Gelidium*
Rhizines absent :
Branch tips with single apical cell (Pl. 24 fig. 3) 4. *Gelidiella*
Branch tips multiaxial :
Branching essentially dichotomous, the branches terete below, compressed above 21. *Gymnogongrus*
Branching not dichotomous :
Medulla pseudoparenchymatous, composed of small thick-walled cells, the subcortical cells larger and with thinner walls 5. *Gelidiopsis*

Medulla evidently filamentous, cortex cells small and compact :
Main axes bearing terete branches with constricted base and long acuminate apex 18. *Agardhiella*
No evident main axes, branches not constricted at the base nor with acuminate tips . 23. *Coelothrix*
Thallus foliaceous or at least in part flattened and more than 1 cm broad, or, if less broad, then tips of branches inrolled :
Thallus with several central axial filaments (not polysiphonous) :
Plants very soft and gelatinous, foliaceous . . . 16. *Platoma*
Plants of firm texture, terete stem continuing into blades as midrib 15. *Cryptonemia*
Thallus with single central axial filament, each cell surrounded by 5 pericentral cells (polysiphonous) :
Midrib conspicuous in main axes and branches, blades ecorticate 35. *Amansia*
Midrib inconspicuous distally, more evident below, blades corticate 36. *Vidalia*

BANGIACEAE

1. *ERYTHROCLADIA* Rosenv.

ERYTHROCLADIA Rosenv. in K. dansk. Vidensk. Selsk. Skr., 7 Raekke, 7 : 71 (1909).

1. ***Erythrocladia subintegra*** Rosenv. in K. dansk. Vidensk. Selsk. Skr., 7 Raekke, 7 : 73 (1909).

Not recorded by author. Description based on Taylor (1960).
Decumbent radial filaments form small epiphytic discs, to 50 μm diam.
Epiphytic on various algae and sea grasses, especially in shallow water.
Unknown locality, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929).
From Bermuda to Brazil.

2. *ERYTHROTRICHIA* Aresch.

ERYTHROTRICHIA Aresch., Phyc. Scand. : 209 (1850), reimpr. in Nova Acta R. Soc. Scient. upsal. 14 : 435 (1850), *nom. cons.*

1. ***Erythrotrichia vexillaris*** (Mont.) Hamel, Annls Cryptog. exot. 2 : 54 (1929).

Porphyra vexillaris Mont., Syll. Gen. Sp. Crypt. : 450 (1856).

Not recorded by author. Description based on Taylor (1960).

Young plants consist of uniseriate filaments attached by their basal cells. Mature plants strap-shaped, to 185 μm broad by 675 μm long, remaining monostromatic, up to 20 μm thick. Basal cell reinforced by rhizoidal branches growing down from cells near base and attaching to substrate.

Epiphytic on coarser algae.
Recorded by Taylor (1960).
From North Carolina to Trinidad.

CHAETANGIACEAE

3. *GALAXAURA* Lamour.

GALAXAURA Lamour. in Nouv. Bull. Soc. philom. Paris 3 : 185 (1812).

KEY TO SPECIES

Thallus terete	1. *G. oblongata*
Thallus flattened	2. *G. marginata*

1. ***Galaxaura oblongata*** (Ell. & Sol.) Lamour., Hist. Polyp. Corall. Flex. : 262 (1816).

Corallina oblongata Ell. & Sol., Nat. Hist. Zoophytes : 114 (1786).

The calcified branches terete, to 1·5 mm diam., the segments 4–17 times as long as their diam. Cortex 60–75 μm wide and of three to four cell layers, the inner cells to 30 μm diam., the outer assimilative cells to 15 μm diam.

Bushy clumps, the plants to 8 cm tall, in sheltered bays from the upper sublittoral to 1·5 m depth.

Balandra Bay, 22 July 1959, *Richardson 443*. Saline Bay, 1 July 1957, *Richardson 88*. Also recorded by Taylor (1960).

From Bermuda to Brazil.

2. ***Galaxaura marginata*** (Ell. & Sol.) Lamour., Hist. Polyp. Corall. Flex. : 264 (1816).

Corallina marginata Ell. & Sol., Nat. Hist. Zoophytes : 115 (1786).

Branching dichotomous, the branches calcified, flattened, to 3 mm broad, the segments to 10 cm long, frequently banded. Cortex 120 μm wide and of two to three cell layers, inner cells to 110 μm diam., assimilative cells to 35 μm diam. by 55 μm long.

Plants to 12 cm tall, from upper sublittoral down to 1·5 m depth.

Balandra Bay, 9 Jan. 1949, *Senior White*, cast ; 22 July 1959, *Richardson 445*. Taparo Point, July 1961, *Richardson 1117*. Unknown locality, 1953, *Bedell 1*.

From Bermuda to Brazil.

GELIDIACEAE

4. *GELIDIELLA* Feldm. & Hamel

GELIDIELLA Feldm. & Hamel in Revue gén. Bot. 46 : 529 (1934).

KEY TO SPECIES

Plants more than 5 cm tall, the erect or arcuate main axes bearing many short peripheral branches (Pl. 21 fig. 1) . . . . 3. *G. acerosa*

Plants less than 5 cm tall, without conspicuous main axes:
  Plants less than 2 cm tall, branches less than 100 μm diam. 1. *G. trinitatensis*
  Plants more than 2 cm tall, branches more than 100 μm diam. . 2. *G. setacea*

1. ***Gelidiella trinitatensis*** W. R. Tayl. in Pap. Mich. Acad. Sci. 28 : 150 (1943).

Not recorded by author. Description based on Taylor (1960).

Plants with terete or compressed erect axes, 1·5 cm tall and 75–90 μm diam., simple or sparingly branched. Erect axes bear terminal or lateral sporangial branches.

On rocks in upper sublittoral.

Manzanilla Point, 14 Apr. 1913, *Thaxter* (Taylor, 1943).

Costa Rica, Trinidad, ? Brazil.

2. ***Gelidiella setacea*** (Feldm.) Feldm. & Hamel in Revue gén. Bot. 46 : 533 (1934). (Plate 24 fig. 3.)

Echinocaulon setaceum Feldm. in Trav. Crypt. déd. L. Mangin : 163 (1931).

Plants 2–3 cm, the branches terete, 120–190 μm diam., growing from single apical cell (Plate 24 fig. 3). Cortex 30 μm wide. No tetrasporangia observed.

On small rocks in lower eulittoral and upper sublittoral.

Carenage, 3 Apr. 1958, *Richardson 312*.

Guadeloupe, French Guiana.

3. ***Gelidiella acerosa*** (Forssk.) Feldm. & Hamel in Revue gén. Bot. 46 : 533 (1934). (Plate 21 fig. 1.)

Fucus acerosus Forssk., Fl. Aegypt.-Arab. : 190 (1775).

Plants wiry, 4–8 cm tall, yellow-brown to dull red, procumbent below, and with erect or arcuate recurved axes, terete to slightly flattened above, 0·5–1 mm diam. (Plate 21 fig. 1). Peripheral branches, 2–7 mm long and 280–325 μm diam. Tetrasporangia (*Richardson 432*, Balandra Bay) 0·5 mm diam. × 1 mm long.

On rocks from eulittoral to depth of 0·5 m.

Balandra Bay, 22 July 1959, *Richardson 432*. Saline Bay, 27 Feb. 1959, *Richardson 348*. Point Radix, 18 July 1957, *Richardson 120*. Also recorded by Taylor (1960).

From Bermuda to Brazil.

5. *GELIDIOPSIS* Schmitz

Gelidiopsis Schmitz in Bot. Jb. 21 : 148 (1895).

1. ***Gelidiopsis planicaulis*** (W. R. Tayl.) W. R. Tayl., Mar. Alg. E. Trop. & Subtrop. Coasts Amer. : 353 (1960).

Wurdemannia miniata var. *planicaulis* W. R. Tayl. in Pap. Mich. Acad. Sci. 28 : 158 (1943).

Not recorded by author. Description based on Taylor (1960).

Plants to 8 cm tall, bushy, tough and wiry in texture. Erect axes sparingly branched, terete near apex but flattened elsewhere and to 1100 μm broad by 185 μm thick. Growth from multi-axial apex, central medulla cells small and thick walled, subcortical cells larger and thinner walled.

Sylvia Bay, 15 May 1938, *Newcombe 789* (Taylor, 1943, as *Wurdemannia miniata* var. *planicaulis*).

Jamaica to Brazil.

6. *GELIDIUM* Lamour.

GELIDIUM Lamour. in Annls Mus. Hist. nat. Paris 20 : 128 (1813), *nom. cons.*

KEY TO SPECIES

Plants small, to 1·5 cm tall, the base creeping ; erect branches simple or sparingly pinnate . . . . 1. *G. pusillum*
Plants larger, freely branched :
  Branches terete . . . . 2. *G. crinale*
  Branches flat :
    Margins of branches minutely serrate . . . . . 5. *G. serrulatum*
    Margins of branches entire :
      Fertile branches in clusters especially on lower parts of plants 4. *G. floridanum*
      Fertile branches not in clusters . . . . . 3. *G. corneum*

1. **_Gelidium pusillum_** (Stackh.) Le Jol. in Mém. Soc. Sci. nat. Cherbourg 10 : 139 (1864).

Fucus pusillus Stackh., Ner. Brit. : 16 (1795).

1a. **_Gelidium pusillum_** var. **_pusillum._**

Growing in short, dense tufts to about 1 cm tall. Erect axes simple or with pinnate branching. Branches to 0·6 mm broad. Rhizines few, subcortical.

From littoral fringe down to upper sublittoral.

Saline Bay, 27 Mar. 1959, *Richardson 368*. Point Radix, 18 July 1957, *Richardson 143*. Also recorded by Taylor (1960).

From Bermuda to Brazil.

1b. **_Gelidium pusillum_** var. **_conchicola_** Piccone & Grun. apud Piccone in Nuovo G. bot. ital. 16 : 316 (1884).

Small tufts creeping on eulittoral rocks, branches less than 5 mm long, to 150 μm diam.

Maqueripe Bay, 15 Aug. 1957, *Richardson 189*. Chupara Bay, 17 June 1957, *Richardson 67*. Matelot, 30 July 1957, *Richardson 173*.

Taylor (1969) described a new species, *Gelidium microdonticum*, to which he referred *Richardson 173* and also a specimen from Maqueripe Bay, *Thaxter*, 1912–13.

2. **Gelidium crinale** (Turn.) Lamour. in Dict. Class. Hist. Nat. 7 : 191 (1825).

Fucus crinalis Turn., Fuci 4 : 4 (1819).

Creeping below, with numerous holdfasts and bearing terete erect branches to 1 cm tall and 500 μm diam. Branches irregularly pinnate, rhizines few.

On rocks of upper sublittoral, rather scattered.

Manzanilla Point, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929). Taparo Point, July 1961, *Richardson 1083*.

From Bermuda to Brazil.

3. **Gelidium corneum** (Huds.) Lamour. in Annls Mus. Hist. nat. Paris 20 : 129 (1813).

Fucus corneus Huds., Fl. Angl., ed. 2 : 585 (1778).

Plants small, not exceeding 5 cm in height, the pinnate to bipinnate branches to over 1 mm broad and 200 μm thick. Rhizines in subcortical region and to lesser extent in outer part of the medulla.

On eulittoral shore in both sheltered and exposed localities.

Maqueripe Bay, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929). Matura Point, 1 July 1957, *Richardson 106*. Point Radix, 18 July 1957, *Richardson 126*. Othoe Point, 6 Feb. 1958, *Richardson 258, 266*.

From Bermuda to Brazil.

4. **Gelidium floridanum** W. R. Tayl. in Pap. Mich. Acad. Sci. 28 : 153 (1943).

Not recorded by author. Description based on Taylor (1960).

Plants to 13 cm tall, erect axes strap-shaped, to 1 mm broad, arising from base of entangled, terete branches. In T.S. of main axes rhizines abundant in subcortical regions. Fertile branches borne in crowded pinnate clusters on the lower parts of main axes.

Maqueripe Bay, Apr. 1912–May 1913, *Thaxter* (Taylor, 1943).

Florida, Trinidad.

5. **Gelidium serrulatum** J. Ag. in Ofvers K. VetenskAkad. Förh. Stockh. 4 : 11 (1847). (Plate 21 fig. 2, Plate 24 fig. 2.)

Plants to 13 cm tall, branching pinnate, the branches flat, to 2 mm broad, very tough. Margins of short peripheral branches minutely serrate. Rhizines subcortical.

In cracks of eulittoral rocks.

Maqueripe Bay, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929). Chupara Bay, 17 June 1957, *Richardson 70*.

Venezuela, Trinidad.

7. *PTEROCLADIA* J. Ag.

Pterocladia J. Ag., Sp. Gen. & Ord. Alg. 2 : 482 (1852).

Key to Species

Branching pinnate, erect axes to 0·5 mm broad	1. *P. bartlettii*
Branching 2–4 pinnate, erect axes more than 0·5 mm broad :	
Main axes remain dominant	3. *P. capillacea*
Main axes divide into several widely spreading divisions	2. *P. americana*

1. ***Pterocladia bartlettii*** W. R. Tayl. in Pap. Mich. Acad. Sci. 28 : 156 (1943).

Creeping branches terete, attached to the rocks by flattened holdfasts. At each holdfast, erect, flattened axes develop, the first to develop simple, the later formed pinnately branched. Most erect axes to 0·5 mm wide and 1·5 cm tall. Pinnate branches to 3 mm long. Rhizines abundant in medulla and inner cortex.

Small, entangled plants on lower eulittoral rocks.

Saline Bay, 27 Feb. 1959, *Richardson 343* ; 24 Apr. 1959, *Richardson 344*.

From Texas to Guadeloupe, Trinidad.

2. ***Pterocladia americana*** W. R. Tayl. in Pap. Mich. Acad. Sci. 28 : 154 (1943).

Not recorded by author. Description based on Taylor (1960).

Erect axes arise from stoloniferous base. Axes 0·5–2·0(–6·0) cm tall, flat, 500–600 μm broad and 75–150 μm thick, simple or sparingly pinnately branched. Tetrasporangia in distal portion of simple axes.

Forming moss-like growth on exposed rocks but taller and more branched in sheltered places, upper sublittoral.

Recorded by Taylor (1960).

From Bermuda to Trinidad.

3. ***Pterocladia capillacea*** (Gmel.) Born. & Thur., Notes Algol. 1 : 57 (1876). (Plate 24 fig. 1.)

Fucus capillaceus Gmel., Hist. Fuc.: 146 (1768).

Plants to 13·5 cm tall. Branching pinnate to tripinnate, the branches to 1·5 mm broad and 0·5 mm thick. Rhizines medullary.

On rocks of lower eulittoral or upper sublittoral.

Maqueripe Bay, Apr. 1912–May 1913, *Thaxter* (Taylor, 1943) ; 15 Aug. 1957, *Richardson 195*. Chupara Bay, 17 June 1957, *Richardson 61*. La Tinta Bay, 20 Jan. 1957, *Richardson 36*.

Hispaniola to Brazil.

The reasons for adopting this name, rather than *P. pinnata* (Huds.) Papenf., used by Taylor (1960) for this species, are given by Dixon (1960).

ENDOCLADIACEAE

8. *ENDOCLADIA* J. Ag.

Endocladia J. Ag. in Linnaea 15 : 449 (1841).

1. ***Endocladia vernicata*** J. Ag. in Linnaea 15 : 449 (1841). (Plate 24 fig. 4.)

Branching dense and wide angled, the segments to about 300 μm diam.

Covering surfaces of midlittoral rocks.

Maqueripe Bay, 15 Aug. 1957, *Richardson 194*. Matelot, 30 July 1957, *Richardson 164*.

Trinidad, Brazil.

RHIZOPHYLLIDACEAE

9. *OCHTODES* J. Ag.

Ochtodes J. Ag. in Acta Univ. lund. 8 (6) : 5 (1872).

1. ***Ochtodes secundiramea*** (Mont.) Howe in Britton & Millsp., Bahama Fl. : 583 (1920). (Plate 21 fig. 3, Plate 24 fig. 6.)

Hypnea secundiramea Mont. in Annls Sci. nat., sér. 2, Bot. 18 : 255 (1842).

Plants bushy, to about 8 cm and profusely, alternately branched. Branches 0·5(–1·5) mm or less in diameter. Two central axial filaments evident in transverse section (Plate 24 fig. 6) and twin apical cells at the branch tips.

From upper sublittoral to 0·5 m depth.

Maqueripe Bay, Apr. 1913, *Thaxter* (Taylor, 1929) ; 15 Aug. 1957, *Richardson 197*. Saline Bay, 1 July 1957, *Richardson 91* ; 24 Apr. 1959, *Richardson 332*.

Bahamas to Trinidad.

CORALLINACEAE

10. *LITHOPHYLLUM* Philippi

Lithophyllum Philippi in Arch. Naturgesch. 3 (1) : 387 (1837).

1. ***Lithophyllum daedaleum*** Fosl. & Howe in Bull. N.Y. bot. Gdn 4 : 133 (1906).

Not recorded by author. Description based on Taylor (1960).

Thin adherent primary crust bearing many short crowded branches, to 6 cm tall and 2 mm thick. Branching subdichotomous, the branches sometimes anastomosing, the apices obtuse, truncate or depressed. Sporangial conceptacles convex, not prominent, about 300 μm diam.

On surf-beaten rocks, lower eulittoral to upper sublittoral.

Recorded by Taylor (1960).

Puerto Rico, Virgin Isles, Trinidad.

11. *AMPHIROA* Lamour.

AMPHIROA Lamour. in Nouv. Bull. Soc. philom. Paris 3 : 186 (1812).

KEY TO SPECIES

Some segments of thallus flattened, with more or less distinct midrib 2. *A. tribulus*

All segments of the thallus terete throughout ; segments end with pad-like swellings 1. *A. fragilissima*

1. **Amphiroa fragilissima** (L.) Lamour., Hist. Polyp. Corall, Flex. : 298 (1816).

Corallina fragilissima L., Syst. Nat., ed. 12, 1 : 1305 (1767).

Plants to 2 cm tall, axes branching dichotomously or trichotomously at the joints. Branch segments terete, 350–700 μm diam., typically swollen at the ends. Conceptacles lateral.

Growing in small entangled clumps from upper sublittoral to 0·5 m depth.

Maqueripe Bay, 15 Aug. 1957, *Richardson 206*. Balandra Bay, 22 July 1959, *Richardson 398*.

From Bermuda to Brazil.

2. **Amphiroa tribulus** (Ell. & Sol.) Lamour., Hist. Polyp. Corall. Flex. : 302 (1816).

Corallina tribulus Ell. & Sol., Nat. Hist. Zoophytes : 124 (1786).

Some segments flattened, to 2 mm broad and with midrib discernible, others terete, 4–6 mm long. Conceptacles numerous on segment faces, to 500 μm diam.

Plants to 2 cm tall on loose stones at about 1 m depth.

Saline Bay, 27 Feb. 1959, *Richardson 385*.

Florida to British Honduras, Trinidad.

12. *CORALLINA* L.

CORALLINA L., Syst. Nat., ed. 10, 1 : 805 (1758).

1. **Corallina officinalis** L., Syst. Nat., ed. 10, 1 : 805 (1758).

Plants tufted with many pinnate branches. The main branches terete, 1·5 mm diam. and with segments to 5 mm long.

A sublittoral species growing to 7 cm tall.

Maqueripe Bay, 15 Aug. 1957, *Richardson 201*. Matelot, 30 July 1957, *Richardson 162*. L'Ainse Nicolas, 12 Aug. 1956, *Richardson 21*. Saline Bay, 27 Feb. 1959, *Richardson 359*. Taparo Point, July 1961, *Richardson 1099*.

Bermuda to Brazil.

GRATELOUPIACEAE

13. *HALYMENIA* Ag.

Halymenia Ag., Syn. Alg. : xix, 35 (1817).

1. ***Halymenia agardhii*** De Toni, Syll. Alg. 4 : 1542 (1905). (Plate 24 fig. 5.)

Branching dichotomous, branches terete, to 10 mm diam. and firmly gelatinous. Dries light brown to pinkish and adheres strongly to paper. Medulla composed of slender filaments frequently radiating from conspicuous stellate 'ganglia'. Inner cortex loosely arranged, outer cortex compact.

Plants to 24 cm tall, only found washed ashore.

Saline Bay, 26 May 1959, *Richardson 404*, cast. St Joseph, 11 July 1957, *Richardson 112*, cast.

Bermuda to Tobago

14. *GRATELOUPIA* Ag.

Grateloupia Ag., Sp. Alg. 1 : 221 (1822).

Key to Species

Thallus simple or sparingly branched, foliaceous and often proliferous . . . 3. *G. cuneifolia*

Thallus much branched, narrow or terete :
  Branching dichotomous, cervicorn or irregular, the branches strap-shaped . . . 2. *G. dichotoma*
  Branching 1–2 pinnate or radial, branches often terete, filiform ; a polymorphic species . . . . 1. *G. filicina*

1. ***Grateloupia filicina*** (Wulf.) Ag., Sp. Alg. 1 : 223 (1822).

Fucus filicinus Wulf. in Jacq., Coll. Bot. 3 : 157 (1789).
Delesseria filicina (Wulf.) Lamour. in Annls Mus. Hist. nat. Paris 20 : 125 (1813).

Main branches terete to somewhat flattened, to 10 mm diam., bearing short (to 3 cm), pinnately or radially arranged branches along their margins. Carposporangia immersed in the thallus, to 180 μm diam. Medulla of anastomosing filaments or branches hollow.

Common widespread species, the largest plants in sheltered localities (*Richardson 354*, Saline Bay), to height of 58 cm. Stunted, poorly developed plants, not exceeding 3·5 cm tall, on rocks of exposed headlands (*Richardson 105*, Matura Point) on the east coast of Trinidad.

Maqueripe Bay, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929). Chupara Bay, 17 June 1957, *Richardson 65, 79*. Matelot, 30 July 1957, *Richardson 181, 182, 183*. L'Ainse Nicolas, 12 Aug. 1956, *Richardson 11*. Saline Bay, 27 Feb. 1959, *Richardson 337, 354* ; 26 May 1959, *Richardson 405*. Matura Point, 1 July 1957, *Richardson 105*.

Manzanilla Point, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929). Point Radix, 18 July 1957, *Richardson 121*. Taparo Point, July 1961, *Richardson 1093*. Los Gallos Point, June 1961, *Richardson 1068*.

North Carolina to Brazil.

2. ***Grateloupia dichotoma*** J. Ag., Alg. Maris Medit. & Adriat. : 103 (1842). (Plate 21 fig. 4.)

Frond branches 2–4·5 mm wide, 300–750 μm thick, branching dichotomous, irregular or cervicorn. Medulla of anastomosing filaments.

Plant from upper sublittoral or sublittoral, to 10 cm tall, brown to yellow-brown in colour.

Maqueripe Bay, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929); 15 Aug. 1957, *Richardson 196*. Chupara Bay, 17 June 1957, *Richardson 62, 78*. Balandra Bay, 22 July 1959, *Richardson 438*. Taparo Point, July 1961, *Richardson 1096, 1102*.

Jamaica to Trinidad.

3. ***Grateloupia cuneifolia*** J. Ag. in Ofvers. K. VetenskAkad. Förh. Stockh. 6 : 85 (1849).

Not recorded by author. Description based on Taylor (1960).

Plants to 40 cm tall, attached by disc-like base. Short stipe divides into a few foliaceous branches, 4–5 cm broad, margins irregularly undulate and often with proliferations. Tetrasporangia scattered, 19 μm diam., 30 μm long.

Maqueripe Bay, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929).

Jamaica to Brazil.

15. *CRYPTONEMIA* J. Ag.

CRYPTONEMIA J. Ag., Alg. Maris Medit. & Adriat. : 100 (1842).

KEY TO SPECIES

Midrib present at least near bases of fronds	2. *C. luxurians*
Midrib absent	1. *C. bengryi*

1. ***Cryptonemia bengryi*** W. R. Tayl., Mar. Alg. E. Trop. & Subtrop. Coasts Amer. : 427 (1960).

Plants 3–7 cm tall, the fronds 15 mm broad and 130(–180) μm thick. Stalk-like portion of fronds to 18 mm long and to 750 μm diam. This may be the juvenile form of *C. luxurians*.

Young specimen from under rock ledge.

Taparo Point, July 1961, *Richardson 1095*.

Jamaica, ? Brazil.

2. ***Cryptonemia luxurians*** (Ag.) J. Ag., Sp. Gen. & Ord. Alg. 2 : 228 (1851). (Plate 23 fig. 4.)

Sphaerococcus lactuca [var.] γ *luxurians* Ag., Sp. Alg. 1 : 232 (1822).

Plants 6–14 cm tall, stipes terete, denuded below, continuing into the fronds as a midrib. The fronds to 15 mm broad, frequently branching, their margins undulate, to 200 μm thick. The main midrib to about 900 μm thick.

Rare species in Trinidad, isolated specimens in fairly sheltered localities along upper sublittoral or in pools.

Matelot, 30 July 1957, *Richardson 188*, cast. Saline Bay, 25 Nov. 1957, *Richardson 241*. Manzanilla Point, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929). Othoe Point, 6 Feb. 1958, *Richardson 279*.

Bermuda to Brazil.

NEMASTOMATACEAE

16. ***PLATOMA*** Schmitz

PLATOMA Schmitz in Nuova Notarisia 5 : 627 (1894).

1. ***Platoma tenuis*** Howe & Taylor in Brittonia 1 : 32 (1931).

Short stipe (to 3 mm) with small basal disc. Fronds foliaceous, gelatinous, to 25 cm long, 20 cm broad, and to 800 μm thick. Medulla filaments 6–15 μm diam.

Cast plants on the shore or free floating in the sea.

Saline Bay, 26 May 1959, *Richardson 407* ; 7 July 1959, *Richardson 415*.

Netherlands Antilles, Brazil.

GRACILARIACEAE

17. ***GRACILARIA*** Grev.

GRACILARIA Grev., Alg. Brit. : liv, 121 (1830), *nom. cons.*

KEY TO SPECIES

Branches flat throughout except for stipes and proliferations :
  Several to many degrees of branching :
    Branches tapering towards base and apex . . . . . 5. *G. foliifera*
    Branches strap-shaped or oblong . . . . . . 6. *G. mammillaris*
  One to few degrees of branching :
    Branches relatively broad, cuneate at the base, with proliferations 7. *G. cuneata*
    Branches narrow, without proliferations . . . . 8. *G. curtissiae*
Branches terete at least near the apices :
  Axes and branches terete throughout . . . . . . 1. *G. verrucosa*
  Main axes usually flattened below, but peripheral branches terete :
    Branching in all planes, the ultimate peripheral branches in dense clusters 2. *G. ferox*

Branching in two planes, marginal, the ultimate branches not in dense clusters :
  Branching pinnate, main axes strap-shaped . . 4. *G. domingensis*
  Branching irregular, axes not strap-shaped . . 3. *G. cervicornis*

1. ***Gracilaria verrucosa*** (Huds.) Papenf. in Hydrobiologia 2 : 195 (1950). (Plate 21 fig. 6.)

Fucus verrucosus Huds., Fl. Angl. : 470 (1762).

Tall slender plants with firm texture to 35 cm tall, the terete branches usually 1–2 mm diam. Cortex 2–3 layers of small cells, the medulla cells 170–465 μm diam. Cystocarps with projecting pericarp, common, 0·4–1 mm diam., 0·4–0·7 mm long.

Growing up from sand-covered rocks in both exposed and sheltered localities in upper sublittoral and to depth of 1·5 m.

Balandra Bay, 15 Mar. 1959, *Richardson 360* ; 22 July 1959, *Richardson 449*. Saline Bay, 7 July 1959, *Richardson 411*. Guayaguayare Bay, 14 Mar. 1960, *Richardson 1001*. Unknown locality, 1953, *Bedell 18*. Also recorded by Taylor (1960).

Bermuda to Brazil.

2. ***Gracilaria ferox*** J. Ag., Sp. Gen. & Ord. Alg. 2 : 592 (1852). (Plate 22 fig. 5.)

Plants bushy, to 10·5 cm tall, branches flat below, to 4 mm broad, terete above and terminating in dense clusters. Medullary cells 155–220 μm diam., surface cells 9–12 μm diam. No cystocarps observed.

Often dominant in lower eulittoral rock pools.

Point Radix, 18 July 1957, *Richardson 125*. Unknown locality, 1953, *Bedell 21*.

Bermuda to Brazil.

3. ***Gracilaria cervicornis*** (Turn.) J. Ag., Sp. Gen. & Ord. Alg. 2 : 604 (1852). (Plate 22 fig. 2.)

Fucus cervicornis Turn., Fuci 2 : 131, t. 121 (1809).

Irregularly branched thallus 12–25 cm tall, seldom more than 3 mm broad and 1·5 mm thick. Short terete branches above. Marginal proliferation. Medulla cells to 390 μm diam. No cystocarps observed.

Growing from the upper sublittoral down to 0·5 m depth.

Matelot, 30 July 1957, *Richardson 161*. L'Ainse Nicolas, 12 Aug. 1956, *Richardson 14*, cast. Petit Trou Bay, 23 Feb. 1960, *Richardson 484*. Scotland Bay, 24 Sept. 1957, *Richardson 213*. Unknown locality, 1952–53, *Bedell*. Also recorded by Taylor (1960).

Bermuda to Brazil.

4. ***Gracilaria domingensis*** (Kütz.) Sonder ex Collins in Proc. Am. Acad. Arts Sci. 37 : 254 (1901). (Plate 21 fig. 5.)

Sphaerococcus domingensis Kütz., Tab. Phyc. 19 : 8, t. 22 fig. a–b (1869).

Plants grow to 35 cm tall, the strap-shaped axes 3(–9) mm broad and 880 μm thick, bearing pinnate branches. Cystocarps 1–25 mm diam.

Widely distributed and common along the upper sublittoral and down to a depth of 1 m, but also occasionally on lower eulittoral rocks.

Matelot, 30 July 1957, *Richardson 149, 158.* Petit Trou Bay, 23 Feb. 1960, *Richardson 483.* Balandra Bay, Feb. 1957, *Richardson 47.* Saline Bay, 1 July 1957, *Richardson 108.* Point Radix, 18 July 1957, *Richardson 127.* Othoe Point, 6 Feb. 1958, *Richardson 270.* Taparo Point, July 1961, *Richardson 1110.* Carenage, 3 Apr. 1958, *Richardson 320*; 17 Feb. 1960, *Richardson 481.* Unknown locality, 1952–53, *Bedell.* Also recorded by Taylor (1960).

Jamaica to Brazil.

5. ***Gracilaria foliifera*** (Forssk.) Børg. in Dansk bot. Ark. 8 (2) : 7 (1932). (Plate 22 fig. 3.)

Fucus foliifer Forssk., Fl. Aegypt.-Arab. : 191 (1775).

Plants to 10·5 cm tall, branching usually dichotomous, the branches to 4 mm broad and 1 mm thick, tapering towards the base and apex. Medulla cells to 450 μm diam. Cystocarps to 1 mm diam. and projecting to 0·8 mm from thallus surface.

In sheltered localities, in rock pools or sublittoral to depth of 1·5 m.

5a. ***Gracilaria foliifera*** var. ***foliifera.***

Manzanilla Point, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929, as *Gracilaria lacinulata*). Guayaguayare Bay, 14 Mar. 1960, *Richardson 1002.*

5b. ***Gracilaria foliifera*** var. ***angustissima*** (Ag.) W. R. Tayl. in Torreya 40 : 193 (1940).

Sphaerococcus multipartitus [var.] δ *angustissimus* Ag., Sp. Alg. 1 : 247 (1822).
Gracilaria multipartita var. *angustissima* (Ag.) Harv. in Smithson. Contr. Knowl. 5 (5) : 107 (1853).

Balandra Bay, 22 July 1959, *Richardson 448.* Saline Bay, 1 July 1957, *Richardson 100.* Carenage, 3 Apr. 1958, *Richardson 318.*

Bermuda to Brazil.

6. ***Gracilaria mammillaris*** (Mont.) Howe in Britton, Fl. Bermuda : 515 (1918).

Rhodymenia mammillaris Mont. in Annls Sci. nat., sér. 2, Bot. 18 : 252 (1842).

Not recorded by author. Description based on Taylor (1960).

Plants 50–100 cm tall, firmly fleshy, irregularly dichotomously branched, the branches flat, 3–5(–10) mm broad. Medulla of thick-walled cells, 50–125 μm diam. Cystocarps scattered, hemispherical.

On upper sublittoral rocks in exposed situations and to depth of 18 m.

Unknown locality Apr. 1952–May 1953, *Bedell.* Also recorded by Taylor (1960).

Bermuda to Brazil.

7. ***Gracilaria cuneata*** Aresch., Phyc. Nov. & Minus Cogn. : 25 (1854), reimpr. in Nova Acta R. Soc. Scient. upsal., ser. 3, 1 : 351 (1855). (Plate 22 fig. 1.)

Plants to 17 cm tall, fronds to 15 mm broad, cuneate at the base and with proliferations along margins. Cystocarps scattered over fronds, 1 mm diam.

On submerged rocks on north coast.

Matelot, 30 July 1957, *Richardson 157, 169*. L'Ainse Nicolas, 12 Aug. 1956, *Richardson 13*.

Venezuela, Brazil.

8. ***Gracilaria curtissiae*** J. Ag. in Acta Univ. lund. 21 (8) : 61 (1886).

Plants to 12·5 cm tall, the dichotomous branches to 11 mm broad, somewhat contracted at the base, 310 μm thick. No cystocarps observed.

A rare plant from sublittoral.

Saline Bay, 7 July 1959, *Richardson 412*.

Florida, Jamaica, Grenada, Trinidad.

SOLERIACEAE

18. *AGARDHIELLA* Schmitz

AGARDHIELLA Schmitz apud Schmitz & Hauptfleisch in Engler & Prantl, Naturl. PflFam. 1 (2) : 371 (1896).

1. ***Agardhiella tenera*** (J. Ag.) Schmitz apud Schmitz & Hauptfleisch in Engler & Prantl, Naturl. PflFam. 1 (2) : 371 (1896). (Plate 22 fig. 4.)

Gigartina tenera J. Ag. in Linnaea 15 : 18 (1841).

Plants 7–27 cm tall, branches terete, 1–1·5 mm diam. with constricted base and long tapering apex. The cortex 150–360 μm wide, composed of small peripheral cells and larger inner cells. Medulla of loose filaments. Cystocarps swollen, embedded, but visible to naked eye, 150–435 μm diam.

On rocks along upper sublittoral or in lower eulittoral pools.

Matelot, 30 July 1957, *Richardson 159*. Saline Bay, 27 Feb. 1959, *Richardson 386*. Othoe Point, 6 Feb. 1958, *Richardson 263*. Taparo Point, July 1961, *Richardson 1085*. Los Gallos Point, June 1961, *Richardson 1066*.

North Carolina to Brazil.

Taylor and Rhyne (1970) discuss the structure of this species at some length.

RHABDONIACEAE

19. *CATENELLA* Grev.

CATENELLA Grev., Alg. Brit. : lxiii, 166 (1830), *nom. cons.*

1. ***Catenella repens*** (Lightf.) Batt. in J. Bot., Lond., 40 (Suppl.) : 69 (1902).

Fucus repens Lightf., Fl. Scot. 2 : 961 (1777).

Light-brown when fresh, drying darker. Plants to 2 cm tall, with frequent branches. The ovoid segments about 3 times as long as broad, 300–400 μm broad, tapering to 150–200 μm where segments join, by 1100–1200 μm long.

Small, creeping, matted plants found in the upper eulittoral and littoral fringe.

Saline Bay, 25 Nov. 1957, *Richardson 243*. Othoe Point, 6 Feb. 1958, *Richardson 250*.

Bermuda to Panama, Brazil.

HYPNEACEAE

20. ***HYPNEA*** Lamour.

HYPNEA Lamour. in Annls Mus. Hist. nat. Paris 20 : 131 (1813).

KEY TO SPECIES

Some branch tips with crozier-like hooks . . . . 3. *H. musciformis*
Branch tips not hooked, either erect or slightly curved :
  Forming dense matted tufts, at least some branches more than 400 μm diam. 1. *H. spinella*
  Forming loose cushions, branches less than 400 μm diam. . 2. *H. cervicornis*

1. ***Hypnea spinella*** (Ag.) Kütz., Sp. Alg. : 759 (1849).

Sphaerococcus spinellus Ag., Sp. Alg. 1 : 323 (1822).

Branches thick, 300–800(–1100) μm diam., growing in all directions. No cystocarps observed.

Forms entangled matted tufts, on rocks and shells, occasionally an epiphyte. From the upper sublittoral to 0·5 m depth.

L'Ainse Nicolas, 12 Aug. 1956, *Richardson 20*. Petit Trou Bay, 23 Feb. 1960, *Richardson 486*. Balandra Bay, 22 July 1959, *Richardson 431, 439, 461*. Unknown locality, 1953, *Bedell 12*. Also recorded by Taylor (1960). Bermuda to Brazil.

2. ***Hypnea cervicornis*** J. Ag., Sp. Gen. & Ord. Alg. 2 : 451 (1852).

Finely branched, delicate habit, the branches less than 400 μm diam. No cystocarps observed.

Forming loose mass in upper sublittoral and lower eulittoral pools in sheltered bay.

Perruquier Bay, 9 Mar. 1958, *Richardson 297*.

Bermuda to Brazil.

3. ***Hypnea musciformis*** (Wulf.) Lamour. in Annls Mus. Hist. nat. Paris 20 : 131 (1813).

Fucus musciformis Wulf. in Jacq., Collect. 3 : 154 (1789).

Recognized by crozier-hooked branch tips. Erect branches to 14 cm tall, most not exceeding 1 mm in diam. Cystocarps observed on a densely branched specimen from Balandra Bay, where the plants were subjected to gentle surf. Cystocarps to 850 μm diam.

Very common plant on all coasts of Trinidad. On rocks in shallow pools 15 cm depth or as epiphyte on other algae from the lower eulittoral to sublittoral.

Chupara Bay, 17 June 1957, *Richardson 76*. Matelot, 30 July 1957, *Richardson 156*. L'Ainse Nicolas, 12 Aug. 1956, *Richardson 18*. Balandra Bay, 22 July 1959, *Richardson 434*. Saline Bay, 1 July 1957, *Richardson 99*. Manzanilla Point, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929). Point Radix, 18 July 1957, *Richardson 145*. Othoe Point, 6 Feb. 1958, *Richardson 259, 260*. Taparo Point, July 1961, *Richardson 1103*. St Pierre, 3 Apr. 1958, *Richardson 324*. Scotland Bay, 24 Sept. 1957, *Richardson 214*. La Tinta Bay, 20 Jan. 1957, *Richardson 40*. Unknown locality, 1953, *Bedell 13*.

Bermuda to Brazil.

PHYLLOPHORACEAE

21. ***GYMNOGONGRUS*** Mart.

GYMNOGONGRUS Mart., Fl. Bras., Enum. Pl. Bras. 1 : 27 (1833).

KEY TO SPECIES

Branches subterete, maximum diameter less than 1 mm . 1. *G. griffithsiae*
Branches narrowly strap-shaped, maximum diameter more than 1 mm 2. *G. tenuis*

1. ***Gymnogongrus griffithsiae*** (Turn.) Mart., Fl. Bras., Enum. Pl. Bras. 1 : 27 (1833).

Fucus griffithsiae Turn., Fuci. 1 : 79 (1808), *'Griffithsii'*.

Plants to 3·5 cm tall, the branches sub-terete, 400 by 750 μm diam., dividing dichotomously. Cystocarps rare, 0·9 mm diam.

On lower eulittoral rocks and along upper sublittoral.

Maqueripe Bay, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929). Saline Bay, 27 Feb. 1959, *Richardson 346*.

North Carolina to Brazil.

2. ***Gymnogongrus tenuis*** J. Ag. in Ofvers K. VetenskAkad. Förh. Stockh. 6 : 88 (1849).

Branching dichotomous, the branches 1–2·5 mm broad. Cystocarps 0·6–0·8 mm diam.

Small stunted plants on eulittoral shore, but to 7 cm tall in sheltered habitats along the upper sublittoral.

Matelot, 30 July 1957, *Richardson 163*. Saline Bay, 27 Feb. 1959, *Richardson 334*. Also recorded by Taylor (1960).

Mexico to Trinidad.

RHODYMENIACEAE

22. *BOTRYOCLADIA* Kylin

BOTRYOCLADIA Kylin in Acta. Univ. lund., Avd. 2, nov. ser. 27 (11) : 17 (1931), *nom. cons.*

1. ***Botryocladia occidentalis*** (Børg.) Kylin in Acta. Univ. lund., Avd. 2, nov. ser. 27 (11) : 18 (1931).

Chrysymenia uvaria var. *occidentalis* Børg. in Dansk bot. Ark. 3 : 403 (1920).

Plants branched, to 16·5 cm tall, the bladder-like branches with very short stalks, almost sessile, 5 mm × 4 mm.

In eulittoral rock pools under overhanging ledges.

Matelot, 30 July 1957, *Richardson 178*. L'Ainse Nicolas, 12 Aug. 1956, *Richardson 27*, cast. Othoe Point, 6 Feb. 1958, *Richardson 280*, cast. Los Gallos Point, June 1961, *Richardson 1079*, cast.

Bermuda to Brazil.

CHAMPIACEAE

23. *COELOTHRIX* Børg.

COELOTHRIX Børg. in Dansk bot. Ark. 3 : 389 (1920).

1. ***Coelothrix irregularis*** (Harv.) Børg. in Dansk bot. Ark. 3 : 389 (1920).

Cordylecladia irregularis Harv. in Smithson. Contr. Knowl. 5 (5) : 156 (1853).

Terete branches of the thallus loosely entangled, to 15 cm long, 0·7 mm diam. Medulla filamentous.

A rare sublittoral species at 1 m depth, growing on small loose rocks.

Saline Bay, 27 Mar. 1959, *Richardson 384*.

Bermuda to British Honduras, Trinidad.

CERAMIACEAE

24. *WRANGELIA* Ag.

WRANGELIA Ag., Sp. Alg. 2 : 136 (1828).

1. ***Wrangelia argus*** Mont., Syll. Gen. Sp. Crypt. : 444 (1856).

Iridescent, plumose branches with main axes to 100 μm diam. Monosiphonous, ecorticate except for a few irregular filaments growing from nodes over main axes. Cells 4–6 times as long as their diameter. Determinate branchlets 20–35 μm diam., to 6 times as long.

Small tufts growing epiphytically on ? *Amphiroa* sp., upper sublittoral.

Balandra Bay, 22 July 1959, *Richardson 433*. Also recorded by Taylor (1960).

Florida to Trinidad.

25. *CERAMIUM* Roth

CERAMIUM Roth, Cat. Bot. 1 : 146 (1797), *nom. cons.*—P. S. Dixon in J. mar. biol. Ass. U.K. 39 : 333 (1960).

1. ***Ceramium floridanum*** J. Ag. in Acta Univ. lund. 30 (7) : 46 (1894).

Plants to 5 cm, branching mostly alternate but occasionally opposite. Main axes 150–185 μm diam., corticated bands at the nodes 90–155 μm broad, of 1–4 rows of cells. Internodes 260–470 μm long. Tetrasporangia 40–50 μm diam.

Epiphytic on *Grateloupia* and *Hypnea musciformis* in lower eulittoral.

Maqueripe Bay, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929). Saline Bay, 27 Feb. 1959, *Richardson 358* ; 24 Apr. 1959, *Richardson 345*.

Florida, Venezuela, Trinidad.

26. *REINBOLDIELLA* De Toni

REINBOLDIELLA De Toni in Memorie R. Ist. veneto Sci. 25 (5) : 35 (1895).

1. ***Reinboldiella repens*** (W. R. Tayl.) Feldm. & Mazoyer in Bull. Soc. Hist. nat. Afr. N. 28 : 219 (1937).

Carpoblepharis repens W. R. Tayl. in Am. J. Bot. 16 : 623 (1929).

Not recorded by author. Description based on Taylor (1960).

Epiphytic, main axes creeping, 5–10 mm long, attached by unicellular holdfasts. Branching alternate, pinnate, the branches to 5 mm long. Both main axes and branches flattened, 165–250 μm diam. Peripheral branches 0·5–2·0 mm long, serrate or with spine-like branchlets 150–200 μm long. Axial filament 80–160 μm diam., completely corticated.

Maqueripe Bay, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929, as *Carpoblepharis repens*).

Trinidad.

27. *CENTROCERAS* Kütz.

CENTROCERAS Kütz. in Linnaea 15 : 731 (1841).

1. ***Centroceras clavulatum*** (Ag.) Mont. in Durieu, Explor. Sci. Algér., Bot. 1 : 140 (1846). (Plate 25 figs. 1–3.)

Ceramium clavulatum Ag. in Kunth, Syn. Pl. 1 : 2 (1822).

Colour varies from purplish to brick-red but bleached specimens often occur. Plants may form dense sward 0·5 cm in height, or loose mass 5·5 cm tall. Filaments to 185 μm diam., internode length to 620 μm. Two specimens (*Richardson 39, 1061*) bore tetrasporangia, 50–60 μm diam.

Common species in Trinidad in both exposed and sheltered localities, frequently in lower eulittoral and upper sublittoral, but also in shade in littoral fringe.

Chupara Bay, 17 June 1957, *Richardson 66*. Matelot, 30 July 1957, *Richardson 153*. Balandra Bay, Feb. 1957, *Richardson 54*; 16 Sept. 1959, *Richardson 463*. Saline Bay, 1 July 1957, *Richardson 81, 95*; 27 Feb. 1959, *Richardson 336*; 27 Mar. 1959, *Richardson 369*. Othoe Point, 6 Feb. 1958, *Richardson 257*. Taparo Point, July 1961, *Richardson 1087*. Los Gallos Point, June 1961, *Richardson 1061, 1075*. Carenage, 3 Apr. 1958, *Richardson 310*. La Tinta Bay, 20 Jan. 1957, *Richardson 39, 43*.

Bermuda to Brazil.

28. ***SPYRIDIA*** Harv.

SPYRIDIA Harv. apud Hook. in Smith, Engl. Fl. 5 (1) : 336 (1833).

KEY TO SPECIES

Branching distichous, smaller lateral branches swollen towards the tips 2. *S. clavata*

Branching irregular; branches not swollen . . . . 1. *S. filamentosa*

1. ***Spyridia filamentosa*** (Wulf.) Harv. apud Hook. in Smith, Engl. Fl. 5 (1) : 337 (1833).

Fucus filamentosus Wulf. in Arch. Bot. Leipzig 3 : 64 (1803); reimpr. ut Crypt. Aquat. : 64 (1803).

Plants bushy, to 5 cm tall, dirty brown. Branching irregular, slender, ultimate branches corticated at the nodes, main branches completely corticated. ? Tetrasporangium, 36 μm diam.

Upper sublittoral along seaward edge of mangrove swamp on rock faces and in mud.

Scotland Bay, 24 Sept. 1957, *Richardson 223*.

Bermuda to Brazil.

2. ***Spyridia clavata*** Kütz. in Linnaea 15 : 744 (1841). (Plate 23 fig. 5, Plate 27 fig. 1.)

To 14 cm tall, axes to 1·5 mm broad, branching distichous, the smaller branches with typical club-shaped tips. Young branches near apex clothed with fine determinate branchlets. Tetrasporangia (*Richardson 256*) 50 μm diam.

Plants scattered in lower eulittoral pools or along upper sublittoral and down to 1·5 m depth.

Balandra Bay, Feb. 1957, *Richardson 46*; 22 July 1959, *Richardson 444*. Saline Bay, 1 July 1957, *Richardson 97*; 27 Mar. 1959, *Richardson 453*. Guayaguayare Bay, 14 Mar. 1960, *Richardson 497*. Othoe Point, 6 Feb. 1958, *Richardson 256*. Taparo Point, July 1961, *Richardson 1092*.

North Carolina to Tobago, Trinidad.

DELESSERIACEAE

29. *CALOGLOSSA* (Harv.) J. Ag.

CALOGLOSSA (Harv.) J. Ag., Sp. Gen. & Ord. Alg. 3 : 498 (1876).

Delesseria subgen. *Caloglossa* Harv. in Smithson. Contr. Knowl. 5 (5) : 98 (1853).

1. ***Caloglossa leprieurii*** (Mont.) J. Ag., Sp. Gen. & Ord. Alg. 3 : 499 (1876).

Delesseria leprieurii Mont. in Annls Sci. nat., sér. 2, Bot. 13 : 196 (1840).

Plants to 3 cm tall and 1·0–1·5 mm broad, branching dichotomous, the thallus constricted at the point of branching and elsewhere to form segments 3–5 mm long. The segments with a distinct midrib consisting of a broad central axial row of large cells developing from a prominent apical cell.

From upper to lower eulittoral but never very common, apparently tolerant of fresh water (*Richardson 116*, Nariva River).

Nariva River, 11 July 1957, *Richardson 116*. Guayaguayare Bay, 14 Mar. 1960, *Richardson 495*. Othoe Point, 6 Feb. 1958, *Richardson 267*.

Bermuda to Brazil.

RHODOMELIACEAE

30. *POLYSIPHONIA* Grev.

POLYSIPHONIA Grev., Scottish Crypt. Fl. 2 : t. 90 (1823), *nom. cons.*

KEY TO SPECIES

Pericentral cells 10–16	3. *P. howei*
Pericentral cells 4(–6) :	
Trichoblasts present, apical cell not notably prominent .	2. *P. ferulacea*
Trichoblasts usually absent, apical cell prominent . .	1. *P. subtilissima*

1. ***Polysiphonia subtilissima*** Mont. in Annls Sci. nat., sér. 2, Bot. 13 : 199 (1840). (Plate 27 figs. 2–3.)

Plants seldom exceeding 1·5 cm, mixed with other algae, e.g. *Centroceras* (*Richardson 492*). Main axes to 90 μm diam. Pericentral cells 4(–6) in number, to 110 μm long and to 40 μm diam. Apical cell conspicuous (Plate 27 fig. 3). Trichoblasts absent.

Inconspicuous plants from eulittoral to upper sublittoral. In both localities apparently tolerant of fresh water.

Nariva River, 11 July 1957, *Richardson 118*. Guayaguayare Bay, 14 Mar. 1960, *Richardson 492*.

Bermuda to Brazil.

2. ***Polysiphonia ferulacea*** Suhr in J. Ag., Sp. Gen. & Ord. Alg. 2 : 980 (1863). (Plate 23 fig. 7.)

Plants to 7 cm, somewhat bushy. Main axes to 250(–420) μm diam., 4(–6) pericentral cells to 250 μm long and 110 μm diam. Trichoblasts present.

On rocks along upper sublittoral and down to 0·5 m depth or in eulittoral pools.

Saline Bay, 27 Feb. 1959, *Richardson 338* ; 26 May 1959, *Richardson 406*. Othoe Point, 6 Feb. 1958, *Richardson 277*.

Bermuda to Venezuela, Trinidad.

3. ***Polysiphonia howei*** Hollenb. apud W. R. Taylor in Allan Hancock Pacif. Exped. 12 : 302 (1945). (Plate 23 fig. 6, Plate 27 figs. 4–5.)

Forming rather dense mats of prostrate filaments bearing erect branches. Axes to 115 μm diam., with 10–12 pericentral cells, to 125 μm long and 25 μm diam. Apex of branches arcuate and with trichoblasts (Plate 27 fig. 5).

Inconspicuous on upper eulittoral rocks, sometimes exposed to surf and spray.

Matura Point, 1 July 1957, *Richardson 107*. Point Radix, 18 July 1957, *Richardson 134*. Guayaguayare Bay, 14 Mar. 1960, *Richardson 493*.

Bermuda to Grenada, Brazil.

31. ***BRYOCLADIA*** Schmitz

BRYOCLADIA Schmitz in Engl. & Prantl., Natürl. PflFam. 1 (2) : 442 (1897).

KEY TO SPECIES

Main axes less than 250 μm diam., pericentral cells less than 80 μm long	2. *B. cuspidata*
Main axes more than 280 μm diam., pericentral cells more than 90 μm long	1. *B. thyrsigera*

1. ***Bryocladia thyrsigera*** (J. Ag.) Falkenb. in Fauna Flora Golf. Neapel 26 : 169 (1901). (Plate 22 fig. 6, Plate 25 figs. 4–5.)

Polysiphonia thyrsigera J. Ag. in Ofvers. K. VetenskAkad. Förh. Stockh. 4 : 17 (1847).

Main axes erect to 8 cm tall, somewhat naked and to 500 μm diam. below, but bushy and much branched and to 300 μm diam. above. Pericentral cells 10, to about 100 μm long. Peripheral branches crowded, alternate or spiral, often recurved. According to Taylor (1960) the shorter branches bear pinnate branchlets but this was not found in the Trinidad specimens. Tetrasporangia (*Richardson 19*) in rows on terminal branchlets to about 60 μm diam.

On rocks in shallow water 0·5 m depth.

Matelot, 30 July 1957, *Richardson 187*. L'Ainse Nicolas, 12 Aug. 1956, *Richardson 19*.

Florida to Brazil.

2. **Bryocladia cuspidata** (J. Ag.) De Toni, Syll. Alg. 4 : 968 (1903). (Plate 22 fig. 7.)

Polysiphonia cuspidata J. Ag. in Ofvers K. VetenskAkad. Förh. Stockh. 4 : 16 (1847).

Plants 3–4 cm tall, forming thin carpet. Erect axes 100–250 μm diam. with pericentral cells to 80 μm long and bearing many polysiphonous branchlets to 1200 μm long and 50–100 μm diam. No tetrasporangia observed.

Common species in Trinidad, often dominant on rock surfaces in lower eulittoral and upper sublittoral.

L'Ainse Nicolas, 12 Aug. 1956, *Richardson 8*. Saline Bay, 27 Feb. 1959, *Richardson 341*. Othoe Point, 6 Feb. 1958, *Richardson 255*. Manzanilla Point, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929). Taparo Point, July 1961, *Richardson 1113*. Los Gallos Point, June 1961, *Richardson 1065*. Carenage, 3 Apr. 1958, *Richardson 311*.

Florida to Brazil.

32. *BRYOTHAMNION* Kütz.

BRYOTHAMNION Kütz., Phyc. Gen. : 433 (1843).

1. **Bryothamnion seaforthii** (Turn.) Kütz., Phyc. Gen. : 433 (1843).

Fucus seaforthii Turn., Fuci 2 : 129 (1809).

Plants 16(–25) cm tall, the main axes compressed, corticate and with 8–9 pericentral cells. Axes bear two rows of pinnate branches, 2–4 mm in length, which in turn bear a few small, spine-like branchlets.

Quite common but never very abundant, in eulittoral rock pools or in shallow water to about 0·5 m depth.

Chupara Bay, 17 June 1957, *Richardson 75*. Matelot, 30 July 1957, *Richardson 170*. L'Ainse Nicolas, 12 Aug. 1956, *Richardson 12*. Saline Bay, 25 Nov. 1957, *Richardson 242*. Manzanilla Point, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929). Taparo Point, July 1961, *Richardson 1114*.

Florida to Brazil.

33. *MURRAYELLA* Schmitz

MURRAYELLA Schmitz in Ber. dt. bot. Ges. 11 : 227 (1893).

1. **Murrayella periclados** (Ag.) Schmitz in Ber. dt. bot. Ges. 11 : 227 (1893). (Plate 27 fig. 6.)

Hutchinsia periclados Ag., Sp. Alg. 2 : 101 (1828).

Plants small, to 1 cm, creeping over rock surface. Main axes polysiphonous, to 105 μm diam., 4 pericentral cells to 120 μm long and to 55 μm diam. Branching radial, the peripheral branches monosiphonous, the cells to 60 μm long by 30 μm diam.

Dominant locally on shaded boulders in upper eulittoral.

Saline Bay, 25 Nov. 1957, *Richardson 236.*

Bermuda to French Guiana.

34. *BOSTRYCHIA* Mont.

BOSTRYCHIA Mont. in Ramon de la Sagra, Hist. Phys. Polit. & Nat. Cuba, Bot., Pl. Cell. : 39 (1842), *nom. cons.*

KEY TO SPECIES

Attachment organs may develop at the apex of any branch of the prostrate system :
- Peripheral branches monosiphonous but the basal segments polysiphonous . . . 2. *B. moritziana*
- Peripheral branches polysiphonous but with the ultimate 1–3 segments monosiphonous . . . . 1. *B. radicans*

Attachment organs develop as outgrowths below the forks of the prostrate system :
- Peripheral branches monosiphonous throughout . . . . 4. *B. tenella*
- Peripheral branches polysiphonous at base but with ultimate 1–3 segments monosiphonous . . . . 3. *B. binderi*

1. ***Bostrychia radicans*** (Mont.) Mont. in Annls Sci. nat., sér.3, Bot. 14 : 286 (1850). (Plate 23 fig. 3, Plate 26 figs. 1–3.)

Rhodomela radicans Mont., op. cit., sér. 2, Bot. 13 : 198 (1840).

Attached by holdfasts which develop at branch apices of creeping axes. Trinidad specimens probably *B. radicans* f. *moniliforme* E. Post (Rev. algol. 9 : 14 (1936)) Plants to 3 cm tall, main axes to 220 μm diam., the monosiphonous axes 30–90 μm diam. A few special branches (stichidia) with polysiphonous stalk and swollen apex in which tetrasporangia develop, the latter 40–60 μm diam. (Pl. 26 fig. 3.)

On rocks, stones, wood and cast iron from eulittoral to upper sublittoral.

Nariva River, 11 July 1957, *Richardson 117.* Point Radix, 18 July 1957, *Richardson 132.* Guayaguayare Bay, 16 Mar. 1960, *Richardson 494.* Othoe Point, 6 Feb. 1958, *Richardson 251, 274.*

Florida to Louisiana, French Guiana, Brazil.

2. ***Bostrychia moritziana*** (Sonder ex Kütz.) J. Ag., Sp. Gen. & Ord. Alg. 2 : 862 (1863).

Polysiphonia moritziana Sonder ex Kütz., Sp. Alg. : 838 (1849).

Not recorded by author. Description based on Taylor (1960).

Plants 2·0–6·5 cm tall, repeatedly pinnately branched. Branches becoming denuded below but closely distichously branched above, the axes with 7–8 pericentral cells, remaining ecorticate. Peripheral branches polysiphonous at base but monosiphonous towards apex.

On mangrove roots in sheltered localities and on rocks in fresh-water streams.

Recorded by Taylor (1960); also recorded from *Thaxter's* collections, Taylor (1929), as *Amphibia moritziana* (Sond.) Kütz. coming from fresh water, 'Maronal [Maraval] Brook in the Senia [? La Seiva] Valley'.

Florida to French Guiana, Trinidad.

3. ***Bostrychia binderi*** Harv., Ner. Austr. : 68 (1849). (Plate 23 fig. 2, Plate 26 fig. 5.)

Attached by holdfasts which develop below forks of creeping axes. Plants to 1·5 cm, forming a mat, main axes about 220 μm diam. Corticate branches generally bipinnate, the curved tips of peripheral branches sometimes monosiphonous for 1–3 segments.

On shaded rocks in the upper eulittoral and the littoral fringe.

Balandra Bay, 22 July 1959, *Richardson 437*. Saline Bay, 25 Nov. 1957, *Richardson 238*. Unknown locality, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929, as *Amphibia sertularia*).

Bermuda to Brazil.

4. ***Bostrychia tenella*** (Vahl.) J. Ag., Sp. Gen. & Ord. Alg. 2 : 869 (1863). (Plate 23 fig. 1, Plate 26 fig. 4.)

Fucus tenellus Vahl in Skr. Naturh.-Selsk. Kiøbenhavn 5 (2) : 45 (1802).

Plants to 3 cm tall, densely tufted. Branches corticate, peripheral branches monosiphonous, to 30 μm diam., the cells to 33 μm long.

On shady littoral rocks but also in lower eulittoral at the exposed station at Matura Point, but on sheltered side of the rocks.

Maqueripe Bay, 15 Aug. 1957, *Richardson 193*. Matura Point, 1 July 1957, *Richardson 104*. Othoe Point, 6 Feb. 1958, *Richardson 248*. Perruquier Bay, 9 Mar. 1958, *Richardson 292*.

Bermuda to Brazil.

35. *AMANSIA* Lamour.

AMANSIA Lamour. in Nouv. Bull. Soc. philom. Paris 1 : 332 (1809).

1. ***Amansia multifida*** Lamour. in Nouv. Bull. Soc. philom. Paris 1 : 332 (1809).

Not recorded by author. Description based on Taylor (1960).

Plants to 15 cm tall, foliaceous, very bushy, attached by small discoid holdfast, stipe terete. Axes regularly pinnately branched, the branches strap-shaped, 2–5 mm broad, branch tips inrolled. The midrib (costa) conspicuous in both main axes and branches, with 5 pericentral cells, flattened wings of branches two cell layers thick.

Recorded by Taylor (1960).

36. *VIDALIA* Lamour. ex J. Ag.

VIDALIA Lamour. ex J. Ag., Sp. Gen. & Ord. Alg. 2 : 1117 (1863), *nom. cons.*

1. ***Vidalia obtusiloba*** (Ag.) J. Ag., Sp. Gen. & Ord. Alg. 2 : 1123 (1863).

Rhytiphlaea obtusiloba Ag., Syst. Alg. : 161 (1824).

Plants to 19 cm tall, axes 4 mm broad, with inrolled branch apices. Axes polysiphonous with 5 pericentral cells, midrib inconspicuous, branches with medulla of two layers of large cells and covered by small-celled cortex.

One record only, from 0·5 m depth.

Matelot, 30 July 1957, *Richardson 168.*

Florida to Brazil.

37. *ACANTHOPHORA* Lamour.

ACANTHOPHORA Lamour. in Annls Mus. Hist. nat. Paris 20 : 132 (1813).

KEY TO SPECIES

Spines present on short lateral branches only, peripheral branches not notably crowded . . . . 2. *A. spicifera*

Spines present on both short lateral branches and main axes, peripheral branches notably crowded . . . . 1. *A. muscoides*

1. ***Acanthophora muscoides*** (L.) Bory in Duperrey, Voy. Monde La Coquille, Bot., Crypt. : 156 (1828).

Fucus muscoides L., Sp. Pl. 2 : 1161 (1753).

Plants to 6 cm tall. Spines clearly evident on both main axes and the short lateral branches. Peripheral branches in crowded clusters.

Along upper sublittoral, mixed with *Acanthophora spicifera.*

Othoe Point, 6 Feb. 1958, *Richardson 269.*

Florida to Brazil.

2. ***Acanthophora spicifera*** (Vahl) Børg. in Bot. Tidsskr. 30 : 201 (1910).

Fucus spiciferus Vahl in Skr. Naturh.-Selsk. Kiøbenhavn 5 (2) : 44 (1802).

Plants 6–14 cm tall, best developed in sheltered localities (*Richardson 207, 306*). Spines confined to the short lateral branches.

Common species often dominant along upper sublittoral, but also from eulittoral and to 0·5 m depth. Also dredged at 2–5 m (Taylor, 1942).

Petit Trou Bay, 23 Feb. 1960, *Richardson 489.* Saline Bay, 1 July 1957, *Richardson 93.* Point Radix, 18 July 1957, *Richardson 130.* Taparo Point, July 1961, *Richardson 1084.* Los Gallos Point, June 1961, *Richardson 1064.* Diego Islands, 18 Apr. 1939, *Taylor 39–486* (Taylor, 1942) ; Carenage, 3 Apr. 1958, *Richardson 306* ; 17 Feb. 1960, *Richardson 477.* Scotland Bay, 24 Sept. 1957, *Richardson 207.* La

Tinta Bay, 20 Jan. 1957, *Richardson 34.* Chacachacare, South Side, 12 Apr. 1961, *Richardson 1049.* Unknown locality, 1953, *Bedell 3.*

Bermuda to Brazil.

38. ***LAURENCIA*** Lamour.

LAURENCIA Lamour. in Annls Mus. Hist. nat. Paris 20 : 130 (1813), *nom. cons.*

KEY TO SPECIES

Peripheral branches short, tubercle-like, crowded ; in T.S. surface cells radially longer than broad, palisade-like . . . . . . 1. *L. papillosa*

Peripheral branches not tubercle-like nor crowded ; in T.S. surface cells appear more or less square :

Plants wiry, drying black . . . . 3. *L. scoparia*

Plants cartilaginous, not notably dark when dried . . 2. *L. gemmifera*

1. **Laurencia papillosa** (Forssk.) Grev., Alg. Brit. : lii (1830). (Plate 23 fig. 8.)

Fucus papillosus Forssk., Fl. Aegypt.-Arab. : 190 (1775).

Plants to 10 cm tall, densely clothed with short branches. The peripheral branches, in transverse section, show an outer layer of cells forming a palisade.

Common species in Trinidad, often associated with *Acanthophora spicifera* and other algae which grow along upper sublittoral of reefs and stony shorelines down to 0·5 m depth.

Balandra Bay, Feb. 1957, *Richardson 58.* Saline Bay, 27 Mar. 1959, *Richardson 378.* Manzanilla Point, Apr. 1912–May 1913, *Thaxter* (Taylor, 1929). Point Radix, 18 July 1957, *Richardson 119, 138.* Othoe Point, 6 Feb. 1958, *Richardson 262.* Taparo Point, July 1961, *Richardson 1091.* Soldado Rock, 30 Apr. 1961, *Richardson 1055.* La Tinta Bay, 20 Jan. 1957, *Richardson 41.*

Bermuda to Brazil.

2. **Laurencia gemmifera** Harv. in Smithson. Contr. Knowl. 5 (5) : 73 (1853).

Not recorded by author. Description based on Taylor (1960).

Plants 10–15 cm tall, cartilaginous, branching alternate, sometimes slightly compressed and distichous, the peripheral branches tubercle-like, 2 mm long. Surface cells of main axes 40–130 μm long, nearly square in section.

On rocks and reefs along upper sublittoral and from 20 m depth.

Recorded by Taylor (1960).

Bermuda to Brazil.

3. **Laurencia scoparia** J. Ag., Sp. Gen. & Ord. Alg. 2 : 746 (1863). (Plate 23 fig. 9.)

Plants to 6(–10) cm tall, very wiry, the branches terete, about 0·5 mm diam. Numerous short peripheral branches.

Dark red-brown clumps from *Sargassum* zone along upper sublittoral.
Balandra Bay, 22 July 1959, *Richardson 436*.
Jamaica to Brazil.

ECOLOGY

The following brief notes have been compiled from observations made during visits to the various localities. Clearly there is much scope for further study of the ecology of the marine algae in Trinidad and it is hoped that this account may stimulate others to examine this neglected field.

Exposed rocky shores (*Matura Point*)

The rocky coastline extending around the north-eastern tip of Trinidad is pounded by heavy Atlantic rollers which are swept shorewards by the prevailing north-easterly trade winds. Under such conditions there is an extensive splash zone above high-water mark. This part of the shore is continuously wetted by spray from breaking seas and a few rather characteristic algae may be found growing on the rocks under these conditions. *Polysiphonia howei* and *Bostrychia tenella* form dense turf-like mats and are mixed with very stunted plants of *Grateloupia filicina*. In contrast the eulittoral, which is actually pounded by the breaking seas, is completely barren and the upper sublittoral only supports a few patches of *Gelidium corneum* turf and stunted plants of *Chaetomorpha* and *Sargassum*.

Sheltered rocky shores (*Saline Bay*)

Terrestrial vegetation frequently impinges directly onto the shore and gives shade to a narrow belt of shoreline along parts of the littoral fringe. A black band sometimes develops at this level and this is due to blue-green algae, frequently intermixed with or just above a turf of *Bostrychia* spp. and *Catenella repens*. Rocks and stones are scattered over the gently sloping shore at Saline Bay. In the upper part of the eulittoral a band of green algae may be recognized. *Enteromorpha* dominates this part of the shore but *Cladophora* and *Chaetomorpha* may also occur (Richardson, 1969). The middle part of the eulittoral is often quite barren but the lower eulittoral is marked by the occurrence of *Acanthophora spicifera*, *Gelidium pusillum* and *Hypnea musciformis*. All these species extend down the shore into the upper sublittoral, where a greater variety of algae may be found, namely *Padina vickersiae*, *Gelidiella acerosa*, *Centroceras clavulatum*, *Grateloupia filicina*, *Struvea anastomosans*, *Bryopsis plumosa*, *Giffordia mitchelliae*, *Dictyota ciliolata*, *Dictyopteris delicatula* and *Bryocladia* spp. The upper sublittoral is marked by the dominance of *Sargassum vulgare*, which often forms a distinct band at this level. Many of the other algae in the upper sublittoral extend out beyond the *Sargassum* but still in shallow water where they are associated with additional species such as *Gracilaria* spp., *Spatoglossum schroederi*, *Caulerpa racemosa*, *Laurencia papillosa*, *Galaxaura oblongata* and *Cladophora* spp.

Sheltered stony shores bordering the Gulf of Paria (Carenage)

Few algae can be found on the stones along the narrow eulittoral shore. A narrow band of stones covered by tufts of *Bachelotia fulvescens* was found along the upper limit of the eulittoral. The same species occurs again on the lower eulittoral shore and extends down into the sublittoral. *Acanthophora spicifera* forms a distinct narrow band which indicates the upper limit of the sublittoral. Just below this level, in shallow water, *Codium isthmocladium, Padina vickersiae* and *P. gymnospora* can be seen to have a sharp upper limit. In slightly deeper water, but still at depths less than 0·5 m, a variety of other algae can be found. They have an irregular and rather scattered distribution since they are attached to those rocks and stones which remain unburied by silt. It is here that *Caulerpa sertularioides, C. verticillata, Dictyota dichotoma, D. divaricata, Rosenvingea intricata, Sargassum filipendula* and *Gelidiella setacea* are associated with some of commoner Rhodophyceae such as *Gracilaria domingensis, Hypnea musciformis, Centroceras clavulatum* and *Bryocladia cuspidata.* The marine angiosperm, *Thalassia testudinum,* covers extensive areas of the silty bottom below 0·5 m depth. Occasional patches of *Ruppia maritima* grow along the upper margins of these *Thalassia* beds. Similar beds are found in sheltered, sandy bays on the east coast.

Rock pools

A few rock pools were found to contain algae. Most of the pools were shallow, less than 15 cm deep, and small in area, 0·1–1·5(–3) sq. m. At Saline Bay and Taparo Point there were a few pools in the upper and middle eulittoral which contained *Enteromorpha* and *Cladophora.* However, most pools were found in the lower eulittoral. At Point Radix an exceptionally deep pool – 36 cm – in the lower eulittoral contained *Gracilaria ferox, G. domingensis, Laurencia papillosa, Cladophora* sp., *Caulerpa fastigiata, Hypnea musciformis, Padina vickersiae, Acanthophora spicifera* and *Grateloupia filicina.* Shallow pools contained the same algae with the exception of *Laurencia,* but with the addition of *Centroceras clavulatum, Sargassum* sp. and *Spatoglossum schroederi.*

The north and north-east coasts of Trinidad are rocky, are exposed to heavy wave action and are bathed by relatively clear waters of fairly constant salinity (19–20‰ Cl). In contrast, the south and west coasts are sandy, silty or swampy, with a few rocky headlands, are not exposed to heavy wave action and are bathed by turbid waters of fluctuating salinities (12–19‰ Cl). It might be expected that such differences in the physical environment would be reflected in floristic differences in the benthic marine algae. This has been confirmed by observation. A few species are widely distributed and common around much of the coastline, namely, *Codium isthmocladium, Grateloupia filicina, Gracilaria domingensis, Hypnea musciformis, Centroceras clavulatum, Bryocladia cuspidata* and *Acanthophora spicifera.* These species were even present in the areas showing the most extreme differences in the physical environment.

A few species appear to be restricted in their distribution, but there is of course always a possibility that they have been overlooked elsewhere. Thus *Dictyota* *dichotoma* has only been found in the north-west, *Bachelotia fulvescens* in the west and south and *Dictyopteris delicatula* in the north and north-east.

Finally, it is evident that many microscopic, epiphytic and calcareous algae remain to be recorded in the future. There are a few other algae which have not been found, but which might be expected to turn up since they have been recorded from neighbouring localities and have a wide distribution throughout the region; these are *Cladophoropsis membranacea, Caulerpa cupressoides, Codium decorticatum, Stypopodium zonale* and *Laurencia obtusa.*

GLOSSARY

acuminate :	tapering gradually to a point
adaxial :	towards the axis or apex
anastomozing :	branches unite where they come into contact and form network
annulate :	surrounded by raised rings or bands
antheridium :	organ (sporangium) in which male sexual cells are produced
arcuate :	curved like a bow
articulated :	jointed
axial :	located along the axis

band :	refers to a horizontal strip of shore which stands out owing to the dominance of one or a few living organisms
belt :	refers to a horizontal strip of shore which is influenced by a particular set of physical conditions

calcareous :	covered with or containing lime
cartilaginous :	firm and gristly
cervicorn :	shaped like a deer's antler
chromatophore :	cell organelle containing pigment
clavate :	club-shaped
coenocytic :	protoplasts not separated by cell walls
conceptacles :	embedded cavities containing sexual reproductive organs
cortex :	outer layers or tissues
corticate :	with external layer(s) of cells
costa :	longitudinal rib
crustose :	forming hard thin brittle crust
cryptostomata :	small pores which represent non-sexual conceptacles
cuneate :	wedge-shaped
cystocarp :	flask-shaped structure arising from carpogonial branch and containing carpospores

decumbent :	prostrate, but with tip rising upwards
dentate :	toothed
determinate :	limited in extent
dichotomous :	divisions into two equal parts

discoid :	flat and circular
distichous :	arranged in two ranks
entire :	with continuous or smooth margin
epiphytic :	living on or attached to another plant
eulittoral :	part of the intertidal shore, the upper and lower limits defined by bands of particular organisms
exposed :	subjected to the physical effects of heavy wave action
fasciculate :	growing in clusters
filament :	slender or thread-like thallus
filiform :	thread-like
foliaceous :	leaf-like in texture or shape
gametangium :	a structure producing sexual cells
ganglion :	refers to the intersection of a number of filaments, like a group of nerve fibres
gelatinous :	texture and consistency of jelly
glaucous :	covered with pale-green bloom
globose :	spherical
hapteron :	holdfast or branch of holdfast
intercalary :	arising between base and apex
lamina :	blade
lanceolate :	tapering to each end
lenticular :	lens-shaped
littoral fringe :	biologically defined region above the eulittoral
medulla :	central spongy tissue
membranous :	thin and semi-transparent
monosiphonous :	with single elongate central tube or filament
monostromatic :	one cell layer thick
mucronate :	abruptly terminated by a short, sharp spine
oogonium :	organ (sporangium) in which female reproductive cells are produced
oosphere :	female sexual cell produced in an oogonium
ovoid :	egg-shaped
palmate :	flattened and branched like the palm of a hand
paraphysis :	sterile filament (associated with sex organs)
peltate :	fixed to the stalk by the centre or by some point within the margin

pericarp :	outer wall of fruiting structure
pericentral :	around the central filament
peripheral :	outermost
pinnate :	arranged on each side of axis
plumose :	feathery
plurilocular :	several chambered
polymorphic :	very variable in form
polysiphonous :	with many elongated tubes
procumbent :	spread over surface of substrate
proliferous :	producing offshoots
pseudoparenchymatous :	resembling parenchymatous tissue

radially :	developing uniformly on all sides
receptacle :	branches bearing reproductive organs
recurved :	bent backwards
rhizine :	thick-walled filament which runs longitudinally in main axis and is continuous with attachment organ
rhizoid :	root-like outgrowth, forming attachment organ

segment :	portion of jointed thallus
septate :	divided by cell walls
serrate :	with sharp more or less straight teeth pointing to apex
sessile :	stalkless
sheltered :	subjected to moderate or no wave action
sorus :	cluster of sporangia
sporangium :	organ in which male or female sexual cells or asexual spores are produced
stellate :	star-like, radiating from a common centre
stipe :	stalk
stoloniferous :	bearing stolons, long slender horizontal branches like runners
sublittoral :	biologically defined region below the eulittoral

tenaculum :	holdfast
terete :	cylindrical, circular in transverse section
tetrasporangium :	sporangium producing tetraspores
tetraspore :	asexual spore borne in groups of four
thallus :	vegetative part of plant body showing little or no differentiation
trabecular :	like a cross-beam
trichoblast :	hair-like branch
truncate :	ending very abruptly as if cut straight across
tubercle :	wart-like projection

undulate :	edges waved upwards and downwards
uniseriate :	arranged in one row

utricle :	bladder-like cell
verticillate :	whorled
vesicles :	bladder-like cavities

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PLATE 16

FIG. 1. *Monostroma oxyspermum* (Kütz.) Doty (*Richardson 491*). Habit of plant.

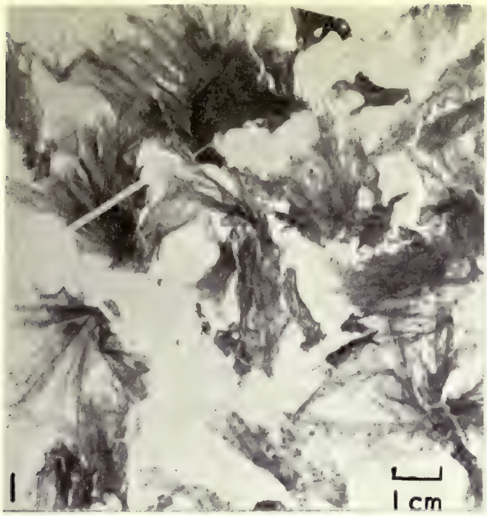
FIG. 2. *Enteromorpha chaetomorphoides* Børg. ((*Richardson 215*). Branched filiform strands 1–3 cells in cross section.

FIG. 3. *Chaetomorpha linum* (O. F. Müll.) Kütz. (*Richardson 240*). Entangled strands of more or less constant width throughout.

FIG. 4. *Chaetomorpha antennina* (Bory) Kütz. (*Richardson 68*). Tufted habit.

FIG. 5. *Chaetomorpha clavata* (Ag.) Kütz. (*Richardson 1112*). Arrow indicates basal cell. Note how filament broadens.

FIG. 6. *Chaetomorpha crassa* (Ag.) Kütz. (*Richardson 1056*). Loose filaments entangled around thallus of *Sargassum*.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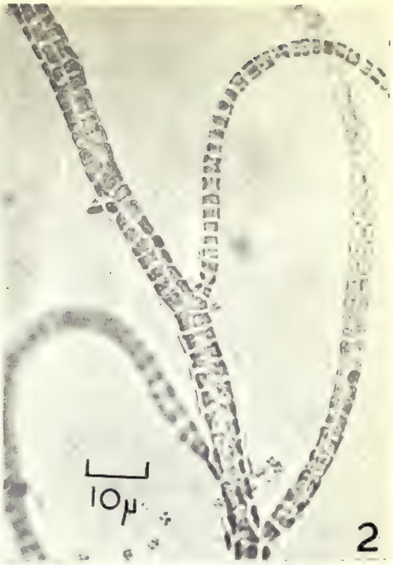
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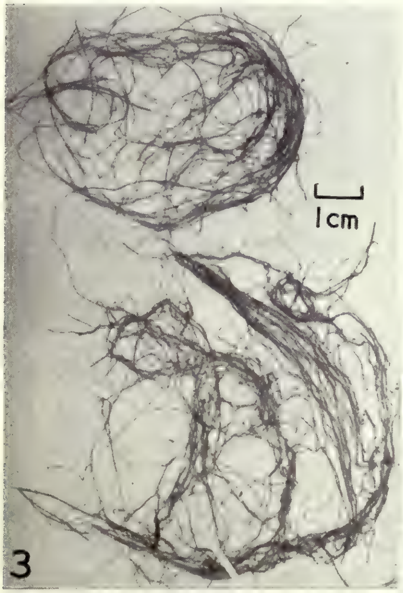
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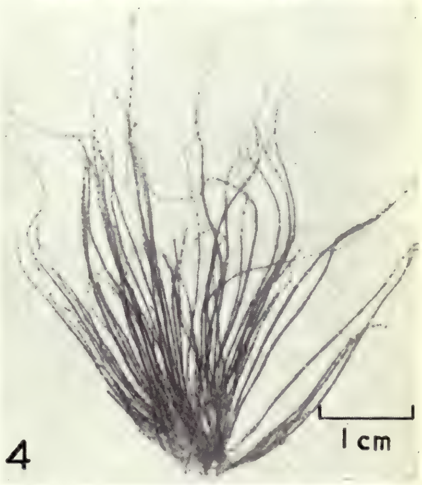
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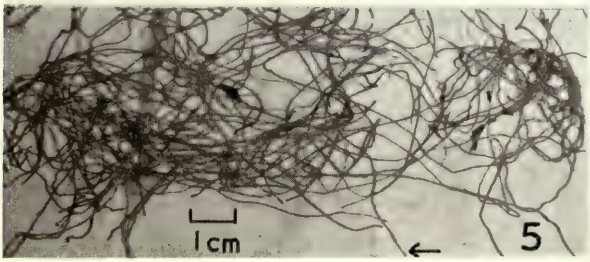
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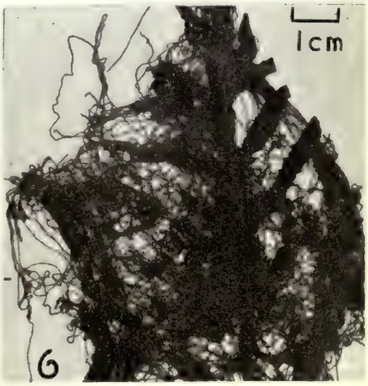
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PLATE 17

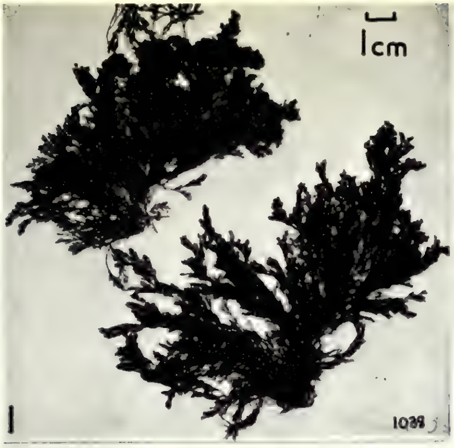
FIG. 1. *Cladophora prolifera* (Roth) Kütz. (*Richardson 1038*). Dense, coarse habit.

FIG. 2. *Cladophora fascicularis* (Mert. ex Ag.) Kütz. (*Richardson 1039*). Rather delicate fasciculate habit.

FIG. 3. *Cladophora coelothrix* Kütz. (*Richardson 294*). Dense turf-like habit.

FIG. 4. *Trichosolen duchassaingii* (J. Ag.) W. R. Tayl. (*Richardson 44*). Dichotomous branching, with hair-like peripheral branches. Free floating plant.

FIG. 5. *Trichosolen duchassaingii* (J. Ag.) W. R. Tayl. (*Richardson 396*). Attached plant.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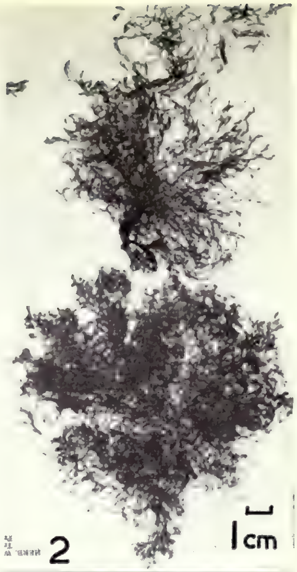
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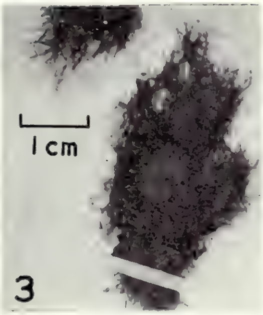
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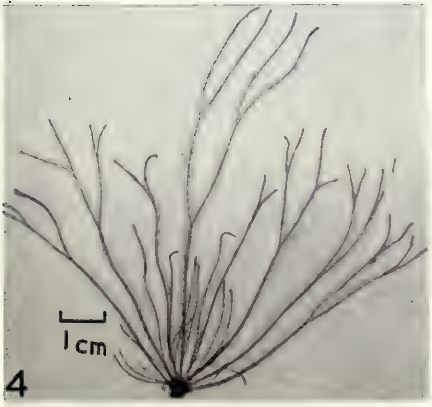
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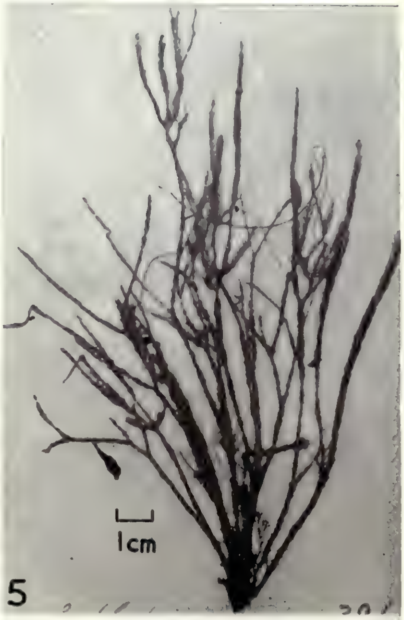
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PLATE 18

FIG. 1. *Boodlea struveoides* Howe (*Richardson 388*). Habit.

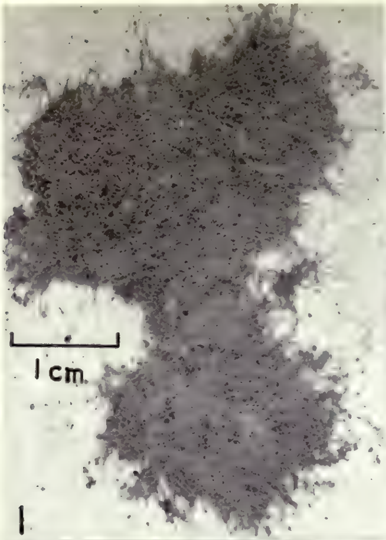
FIG. 2. *Rhizoclonium riparium* forma *validum* Foslie (*Richardson 249*). Rhizoidal branch which has attached itself to neighbouring filament.

FIG. 3. *Struvea anastomosans* (Harv.) Picone (*Richardson 351*). Habit.

FIG. 4. *Siphonocladus tropicus* J. Ag. (*Richardson 458*). Bushy habit.

FIG. 5. *Ernodesmis verticillata* (Kütz.) Børg. (*Richardson 52*). Whorls of branches.

FIG. 6. *Codium repens* Crouan frat. ex Vickers (*Richardson 176*). Decumbent habit.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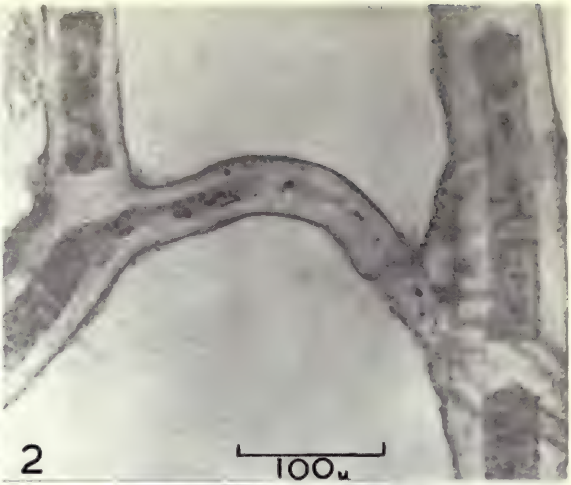
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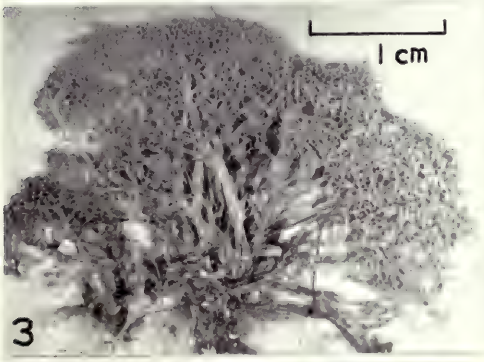
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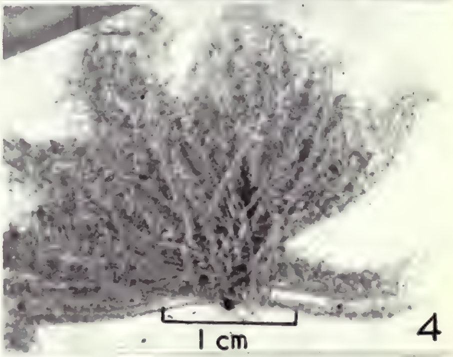
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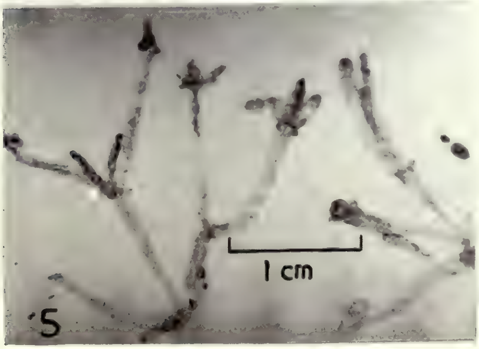
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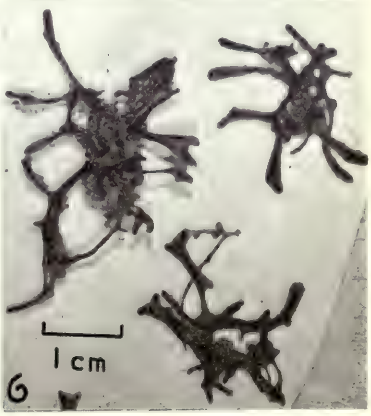
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PLATE 19

FIG. 1. *Boodlea struveoides* Howe (*Richardson 388*). Showing network of branches with tenacula (arrowed) joining neighbouring segments.

FIGS. 2, 3. *Ectocarpus breviarticulatus* J. Ag. (*Richardson 1135*). Fig. 2 : plurilocular sporangium. Fig. 3 : habit.

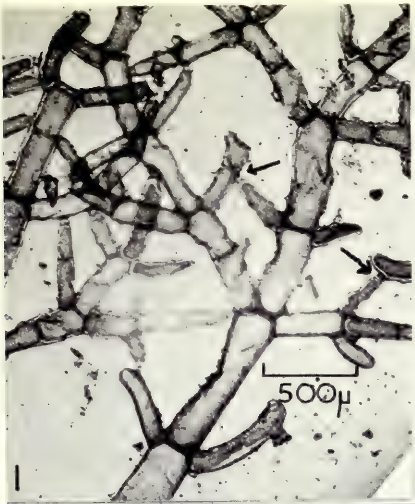
FIG. 4. *Bachelotia antillarum* (Grun.) Gerloff (*Richardson 309*). Cells of filament with paired chromatophores, stellate in living condition but distorted, probably by preservative.

FIG. 5. *Sphacelaria tribuloides* Menegh. (*Richardson 403*). Branched filament bearing triangular propagule.

FIG. 6. *Ectocarpus breviarticulatus* J. Ag. (*Richardson 1135*). Hooked branch tips.

FIG. 7. *Lobophora variegata* (Lamour.) Womersl. (*Richardson 373*). Transverse section of thallus showing young sporangial sori with indusium and central medulla cells.

FIG. 8. *Padina vickersiae* Hoyt (*Richardson 155*). Transverse section of the thallus showing two bands of sporangia and broken indusium (arrowed).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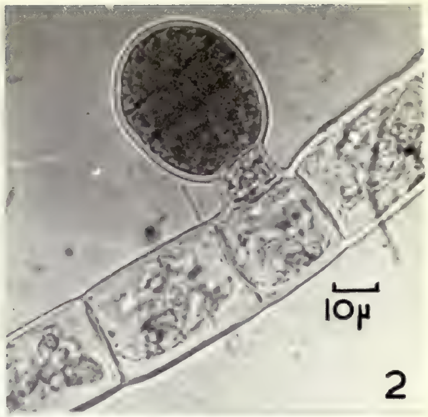
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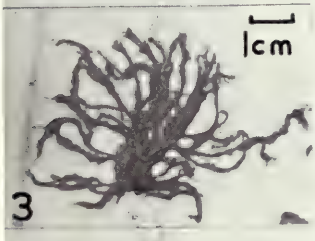
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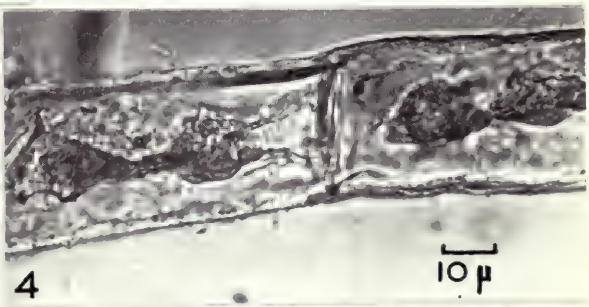
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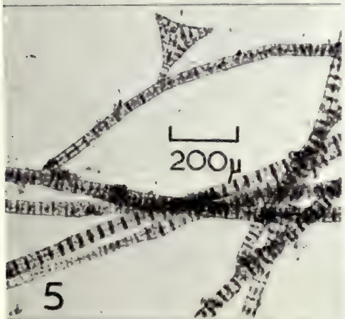
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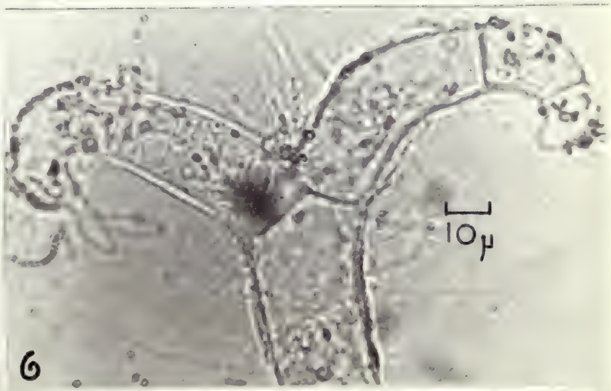
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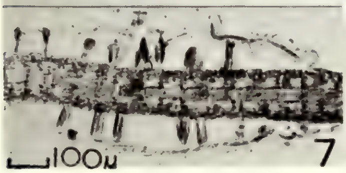
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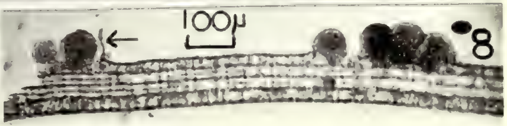
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PLATE 20

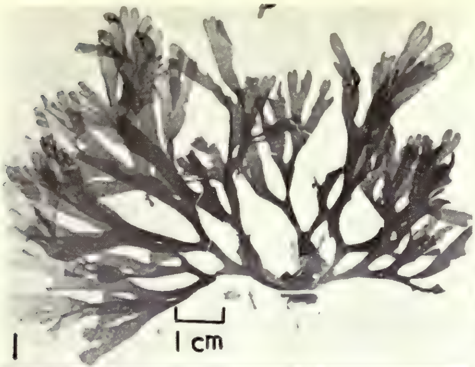
FIG. 1. *Dictyota dichotoma* (Huds.) Lamour. (*Richardson 319*). Habit.

FIG. 2. *Dictyota cervicornis* Kütz. (*Richardson 208*). Habit of mature plant with cervicorn branching.

FIG. 3. *Dictyota ciliolata* Kütz. (*Richardson 382*). Habit of exceptionally broad specimen.

FIG. 4. *Padina gymnospora* (Kütz.) Vickers (*Richardson 474*). Inrolled apical margin and sporangial bands flanked by pairs of hair bands.

FIGS. 5–7. *Sargassum desfontainesii* (Turn.) Ag. (*Richardson 1044*). Fig. 5 : habit. Fig. 6 : branched receptacle, one branch bearing a vesicle. Fig. 7 : oospheres (eggs) extruded from the terminal conceptacles.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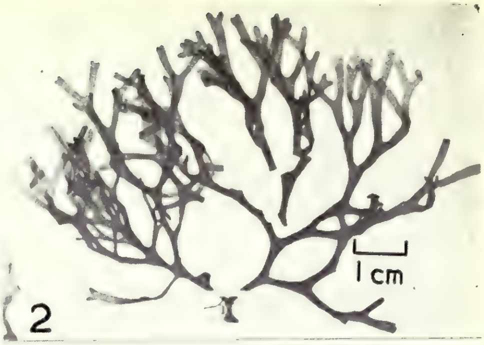
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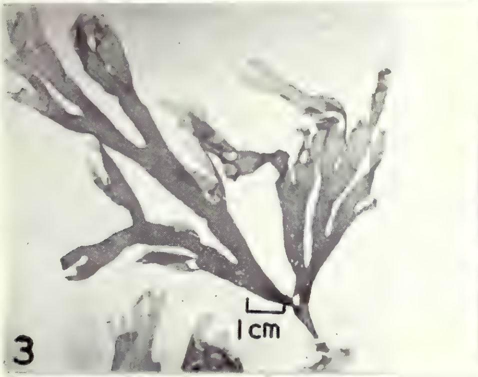
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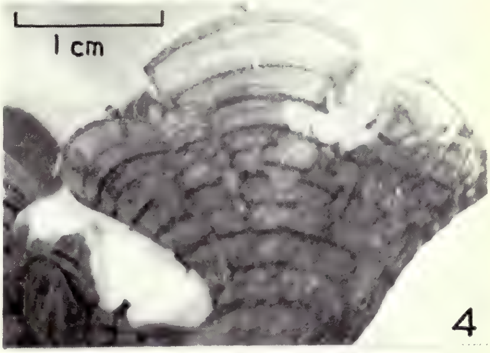
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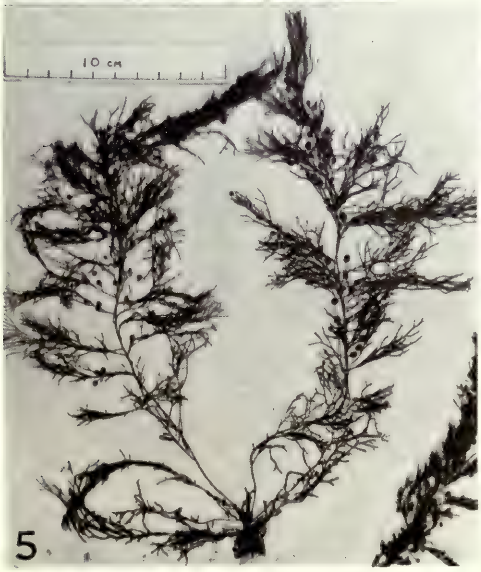
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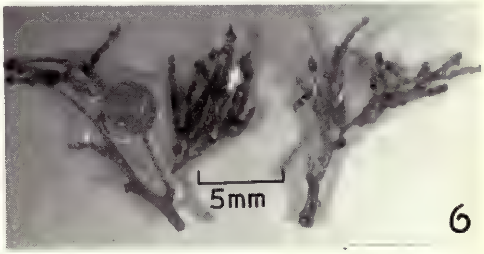
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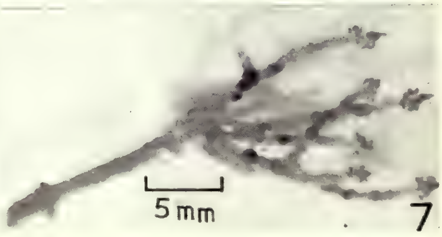
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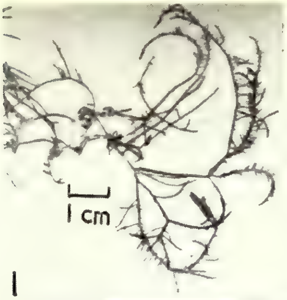
PLATE 21

Fig. 1. *Gelidiella acerosa* (Forssk.) Feldm. & Hamel (*Richardson 120*). Arcuate habit.
Fig. 2. *Gelidium serrulatum* J. Ag. (*Richardson 70*). Habit.
Fig. 3. *Ochtodes secundiramea* (Mont.) Howe (*Richardson 197*). Habit.
Fig. 4. *Grateloupia dichotoma* J. Ag. (*Richardson 196*). Habit.
Fig. 5. *Gracilaria domingensis* (Kütz.) Sonder ex Collins (*Richardson 320*). Habit.
Fig. 6. *Gracilaria verrucosa* (Huds.) Papenf. (*Richardson 360*). Habit.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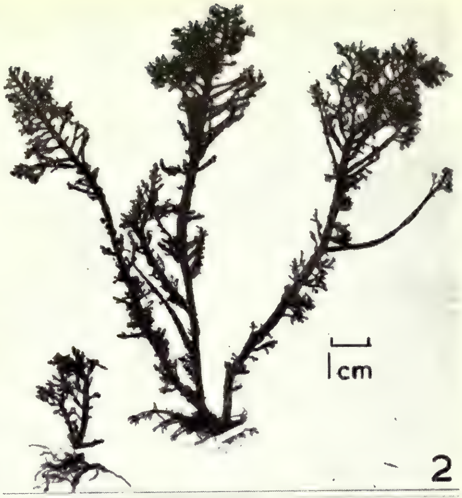
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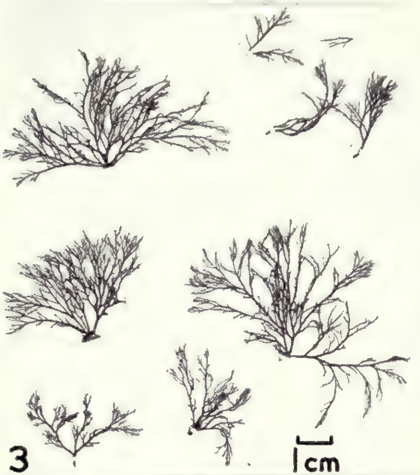
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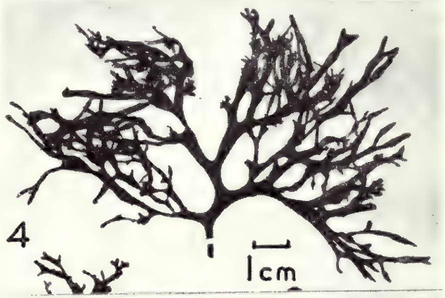
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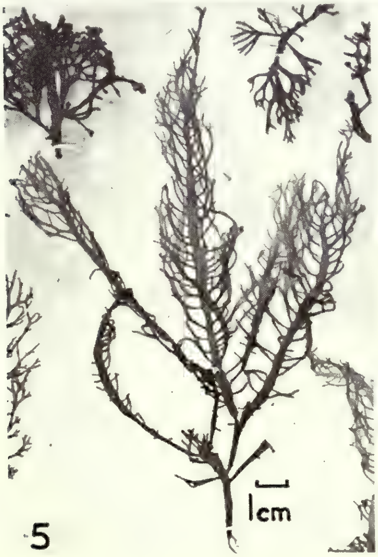
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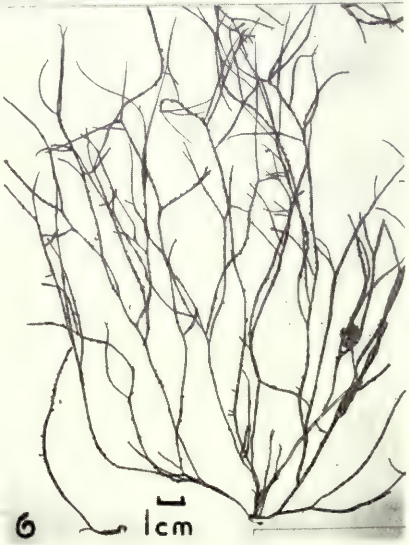
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PLATE 22

FIG. 1. *Gracilaria cuneata* Aresch. (*Richardson 157*). Broad, flat form of thallus.

FIG. 2. *Gracilaria cervicornis* (Turn.) J. Ag. (*Richardson 213*). Branching in two planes, otherwise irregular.

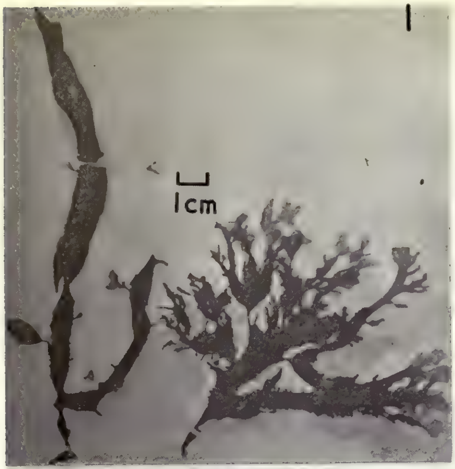
FIG. 3. *Gracilaria foliifera* (Forssk.) Børg. (*Richardson 1002*). Segments taper towards base and apex.

FIG. 4. *Agardhiella tenera* (J. Ag.) Schmitz (*Richardson 386*). The base of branches constricted, the apices long acuminate.

FIG. 5. *Gracilaria ferox* J. Ag. (*Richardson 125*). Branching in all planes, ultimate branchlets congested.

FIG. 6. *Bryocladia thyrsigera* (J. Ag.) Falkenb. (*Richardson 19*). Habit.

FIG. 7. *Bryocladia cuspidata* (J. Ag.) De Toni (*Richardson 341*). Habit, showing main axes clothed with short branchlets.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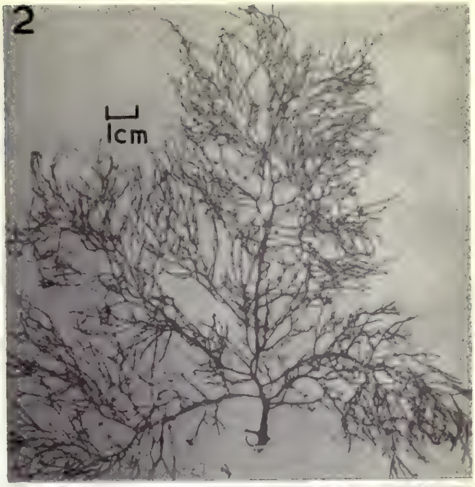
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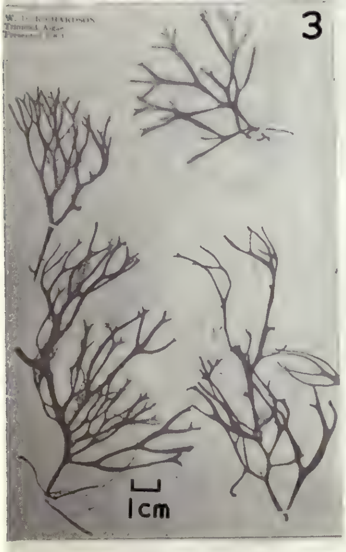
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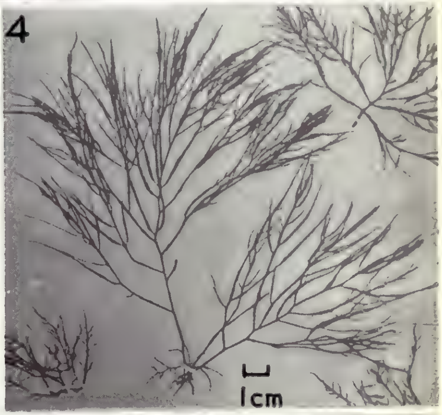
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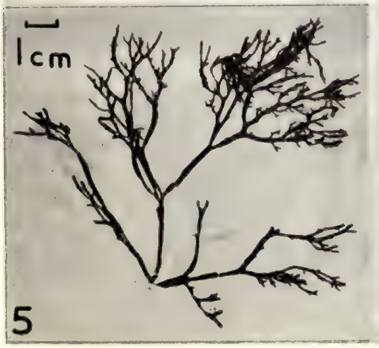
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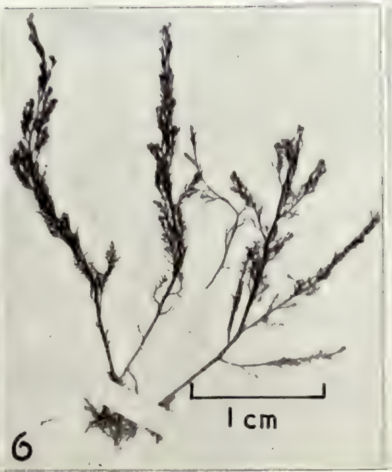
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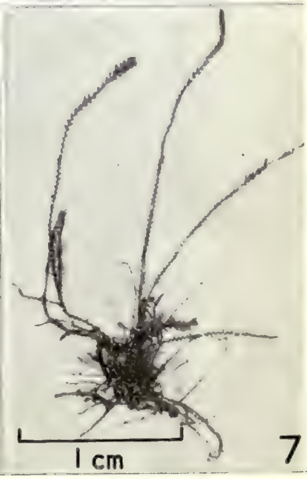
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PLATE 23

FIG. 1. *Bostrychia tenella* (Vahl) J. Ag. (*Richardson 104*). Habit.

FIG. 2. *Bostrychia binderi* Harv. (*Richardson 238*). Habit.

FIG. 3. *Bostrychia radicans* (Mont.) Mont. (*Richardson 274*). Habit.

FIG. 4. *Cryptonemia luxurians* (Ag.) J. Ag. (*Richardson 279*). Habit.

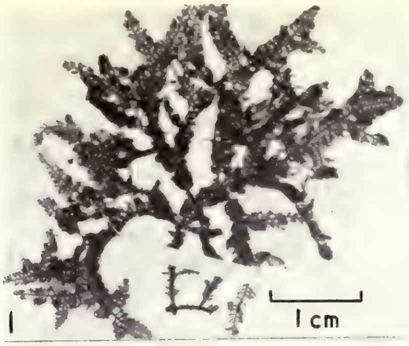
FIG. 5. *Spyridia clavata* Kütz. (*Richardson 497*). Habit.

FIG. 6. *Polysiphonia howei* Hollenb. (*Richardson 493*). Mat-like habit.

FIG. 7. *Polysiphonia ferulacea* Suhr (*Richardson 277*). Habit.

FIG. 8. *Laurencia papillosa* (Forssk.) Grev. (*Richardson 262*). Habit; crowded short branchlets.

FIG. 9. *Laurencia scoparia* J. Ag. (*Richardson 436*). Habit.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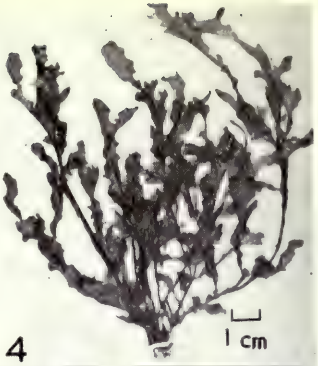
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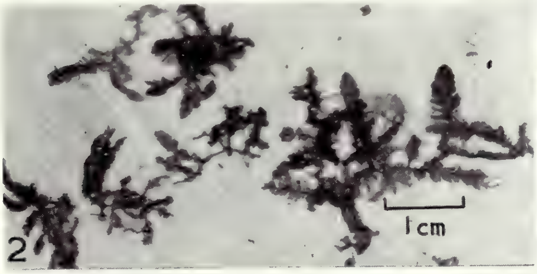
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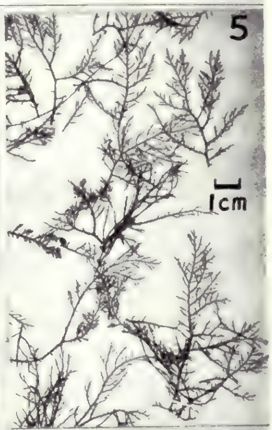
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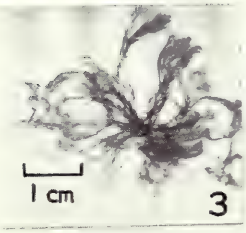
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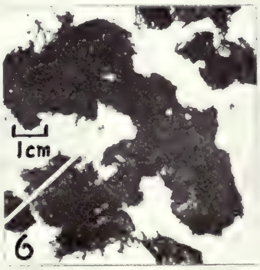
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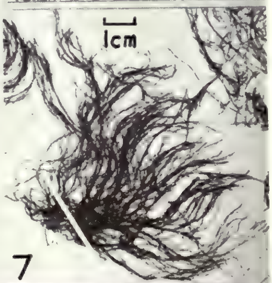
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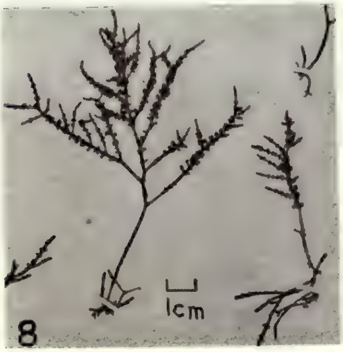
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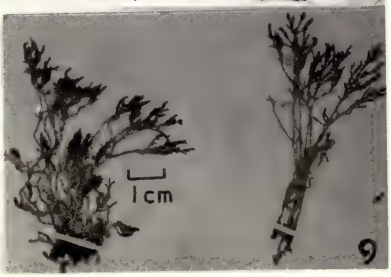
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PLATE 24

FIG. 1. *Pterocladia capillacea* (Gmel.) Born. & Thur. (*Richardson 61*). Transverse section of thallus showing medullary rhizines (arrow).

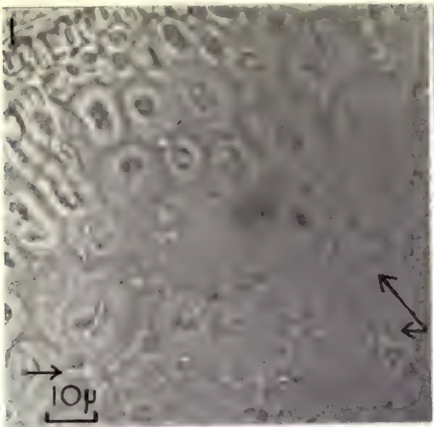
FIG. 2. *Gelidium serrulatum* J. Ag. (*Richardson 70*). Transverse section of thallus showing sub-cortical rhizines (arrow).

FIG. 3. *Gelidiella setacea* (Feldm.) Feldm. & Hamel (*Richardson 312*). Single apical cell.

FIG. 4. *Endocladia vernicata* J. Ag. (*Richardson 194*). Single apical cell dividing by oblique cross walls.

FIG. 5. *Halymenia agardhii* De Toni (*Richardson 112*). A stellate ganglion from the medulla.

FIG. 6. *Ochtodes secundiramea* (Mont.) Howe (*Richardson 197*). Transverse section of thallus showing biaxial structure (arrow).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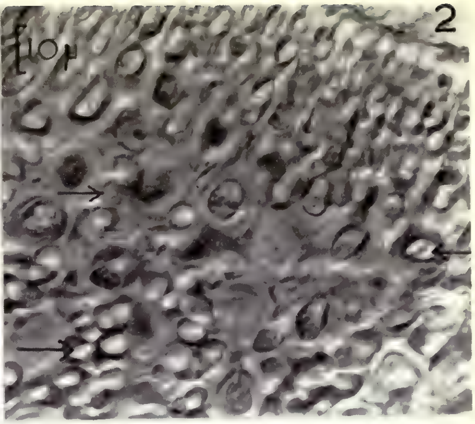
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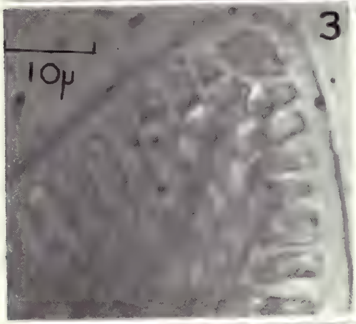
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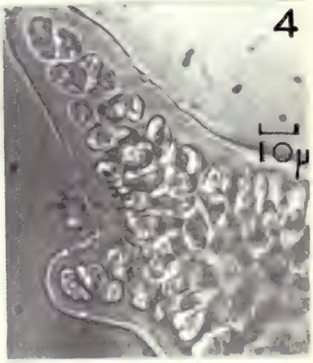
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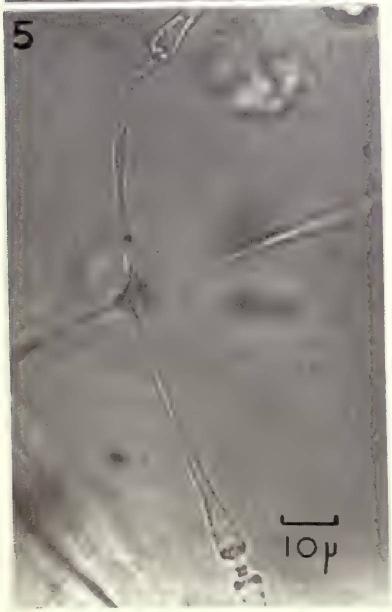
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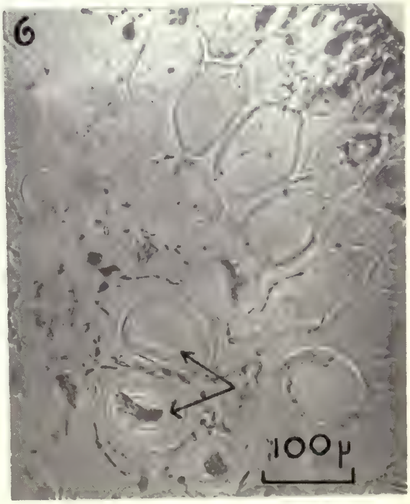
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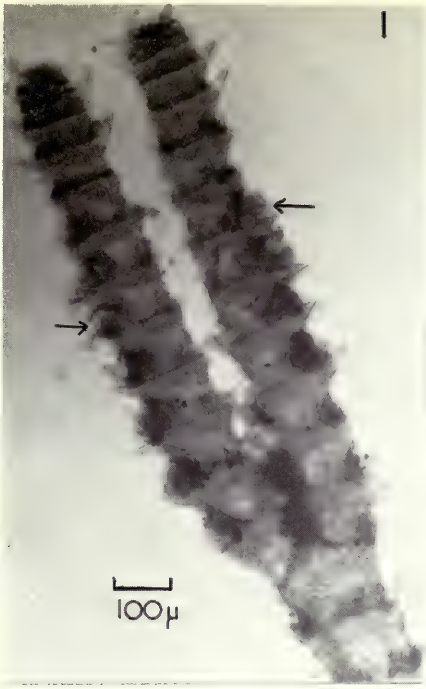
PLATE 25

Figs. 1–3. *Centroceras clavulatum* (Ag.) Mont. (*Richardson 257*). Fig. 1 : branch apex showing whorls of spines and tetrasporangia (arrows). Fig. 2 : apex of single branch showing apical cell. Fig. 3 : single spine.

Figs. 4, 5. *Bryocladia thyrsigera* (J. Ag.) Falkenb. (*Richardson 19*). Fig. 4 : short erect polysiphonous branches. Fig. 5 : apex of filament with trichoblasts which are deciduous.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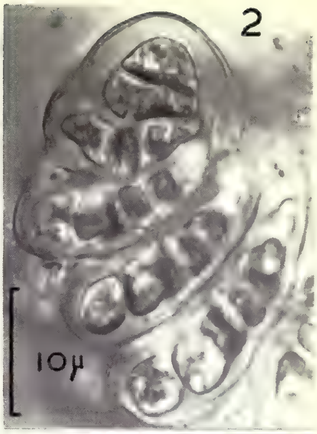
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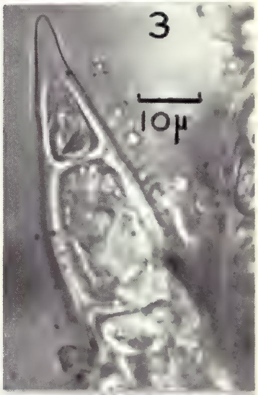
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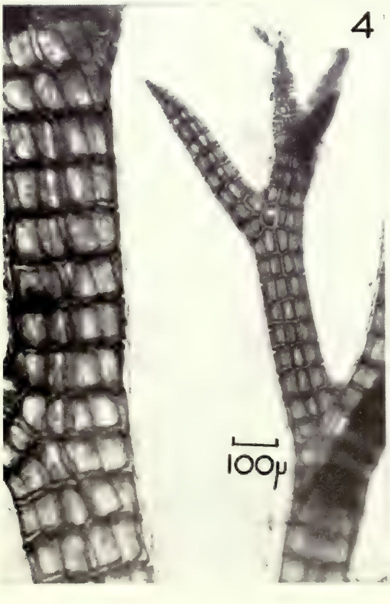
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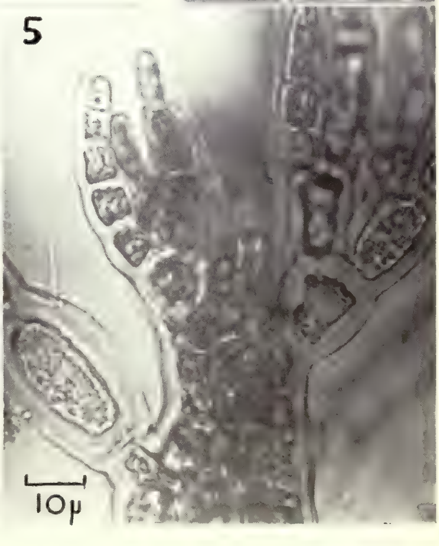
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PLATE 26

FIGS. 1-3. *Bostrychia radicans* (Mont.) Mont. (*Richardson 274*). Fig. 1: incurved branch tips. Fig. 2: haptera developing in ordinary branch positions. Fig. 3: tetrasporangial stichidium.

FIG. 4. *Bostrychia tenella* (Vahl) J. Ag. (*Richardson 104*). Apical part of shoot showing long monosiphonous branch tips.

FIG. 5. *Bostrychia binderi* Harv. (*Richardson 238*). Apical part of shoot, showing branching in two rows, branches polysiphonous except for ultimate tip of branchlets.

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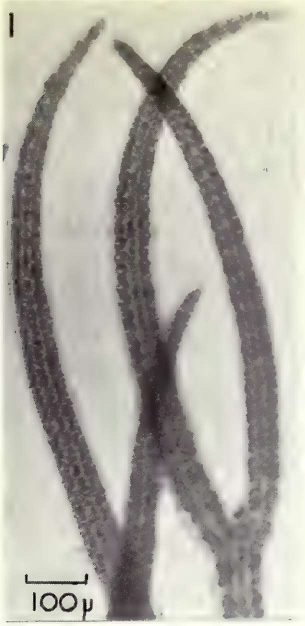

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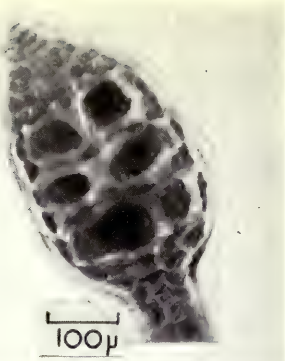

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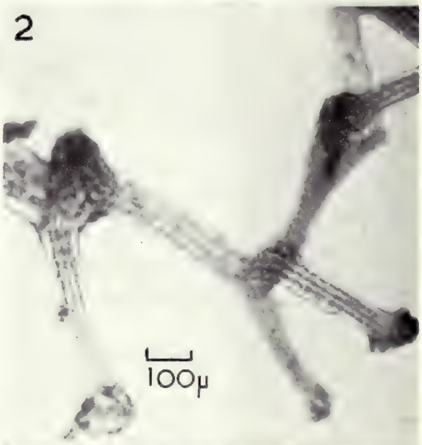

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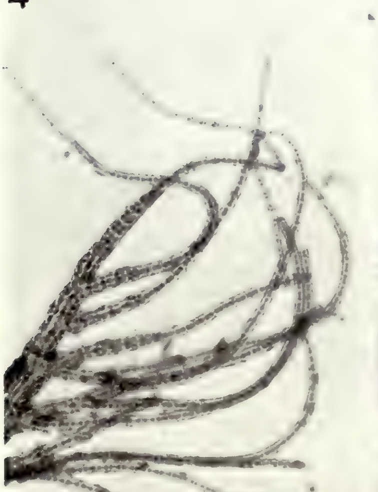

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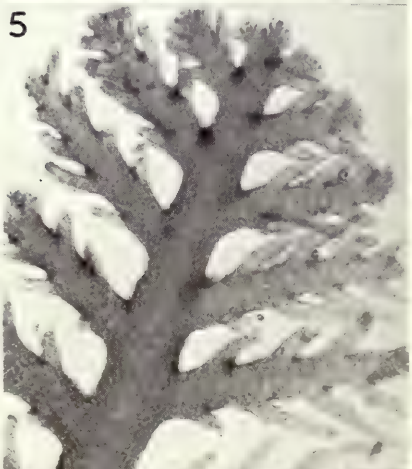


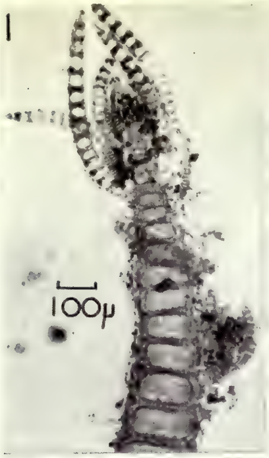
PLATE 27

FIG. 1. *Spyridia clavata* Kütz. (*Richardson 497*). Nodal cortication of ultimate branchlets, but indeterminate (main) axis is fully corticated.

FIGS. 2, 3. *Polysiphonia subtilissima* Mont. (*Richardson 118*). Fig. 2 : four pericentral cells, no trichoblasts. Fig. 3 : prominent apical cell.

FIGS. 4, 5. *Polysiphonia howei* Hollenb. (*Richardson 493*). Fig. 4 : tetrasporangiate branches. Fig. 5 : trichoblasts.

FIG. 6. *Murrayella periclados* (Ag.) Schmitz (*Richardson 236*). Monosiphonous ultimate branchlets radially organized.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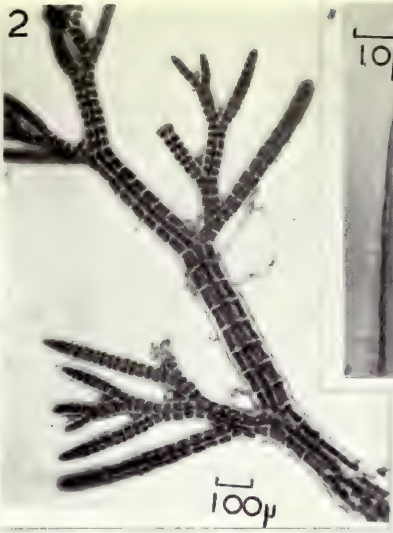
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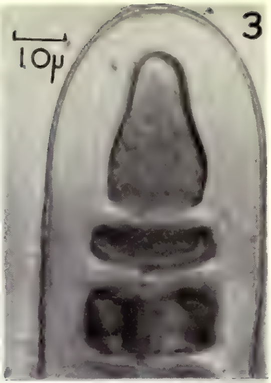
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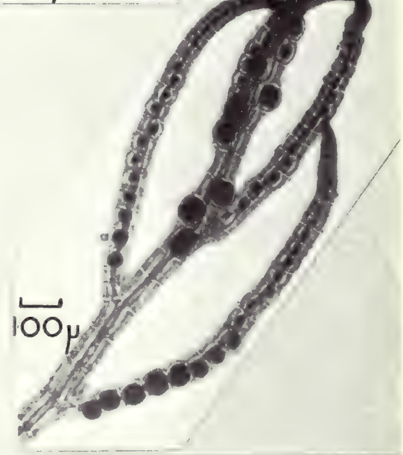
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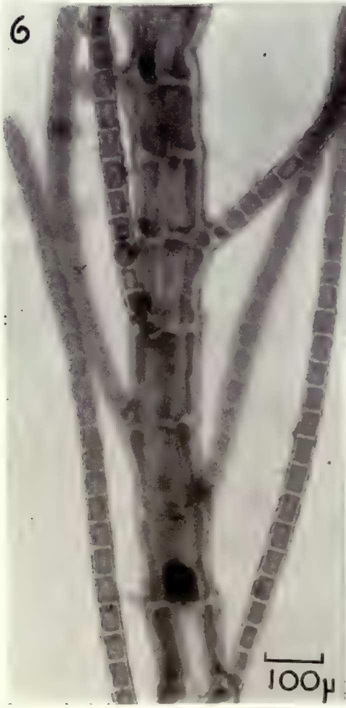
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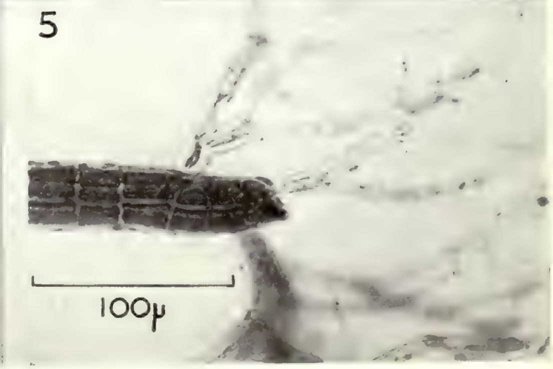
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C. J. HUMPHRIES

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BOTANY Vol. 5 No. 4
LONDON: 1976

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CHRISTOPHER JOHN HUMPHRIES

Pp. 145–240 ; 26 *Text-figures, Plates* 28–29

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A REVISION OF THE MACARONESIAN GENUS *ARGYRANTHEMUM* WEBB EX SCHULTZ BIP. (COMPOSITAE-ANTHEMIDEAE)

By C. J. HUMPHRIES

SUMMARY

The woody endemic Macaronesian genus *Argyranthemum* is revised. In all, 22 species, grouped into five sections, are recognized, all of which occur in the North Atlantic insular archipelagos of Madeira, the Salvage Islands and the Canary Islands. The generic status and the history of taxonomic treatments in the genus *Argyranthemum* are discussed in relation to other Anthemidean genera of the Chrysanthemum complex. A key to all species and subspecies is given, each taxon is fully described and relevant taxonomic characters are discussed in some detail. Full synonomy is cited and notes on distribution and ecology are provided. Distribution maps for all taxa occurring in the Canary Islands and Madeira are provided excluding only *A. thalassophilum* (Svent.) C. J. Humphries, which occurs in the Salvage Islands. Five new species : *A. lemsii*, *A. haouarytheum*, *A. sventenii*, *A. lidii*, *A. hierrense*, and two new subspecies : *A. frutescens* subsp. *pumilum* and *A. broussonetii* subsp. *gomerense* have been described from the Canary Islands and 22 new combinations are made. The relationship between the different sections and their correlation with ecology and vegetation zones is discussed in detail with particular reference to the Canary Islands.

INTRODUCTION

THE genus *Argyranthemum* is one of a taxonomically difficult group of genera in the Chrysanthemum complex, consisting of 22 closely related species, endemic to Madeira, the Salvage Islands and the Canary Islands.

The taxonomic problems in the genus are due to two main factors, the first being the question of its relationships with other genera in the Chrysanthemum complex, and secondly the classification of narrow endemics which have locally evolved in response to diversity of climatic and habitat conditions in the northern Macaronesian archipelagoes.

Only fairly recently has it been possible, on the basis of differences in morphology, embryo-sac development, fruit anatomy, phytochemistry and distribution data, to recognize the species clusters within the Chrysantheminae. Previous generic classifications were based on one or two unreliable technical characters and tended to fall into two main schools of treatment. At one extreme, for example, the genus *Argyranthemum* was divided up into five distinct genera (Schultz Bipontinus, 1844a) and at the other extreme was included as a small section in a large heterogeneous genus *Chrysanthemum* L. (Bentham, 1873 ; Hoffman, 1889–1894).

The lack of information on the Macaronesian species has made the need to review the genus an urgent task in the light of modern taxonomic studies, which have been centred largely on European and Oriental taxa. To present the right context for discussion of generic delimitation in *Argyranthemum* it has been considered appropriate to include an historical account of this and closely related genera.

The last major taxonomic treatment of infrageneric variation in *Argyranthemum* was carried out by Schultz Bipontinus (1844a). Since that time there have been a number of important collections from the Macaronesian Islands (and particularly from the Canary Islands) such as those of Bourgeau (1844, 1855), Pitard (1905–1906), Sventenius (1947–1973), Lems (1957–1966) and Bramwell (1968–1969), which have included material of *Argyranthemum* ; but undoubtedly, lack of herbarium material has still been a major problem for a comprehensive review. This revision is based mainly on my own collections and field studies in the Canary Islands and includes some data from morphological and cytological studies and biometrical information from comparative cultivation.

The Madeiran species of *Argyranthemum*, especially the polymorphic *A. pinnatifidum* (L. f.) Lowe, are poorly understood. Few specimens are available and none of the species are in cultivation. Generally I have followed Lowe's treatments (1838, 1868), but have included my own data from more recently collected specimens from a number of European herbaria.

The taxonomic section contains descriptions and keys to all taxa, synonomy and nomenclatural notes where relevant, typifications to all taxa, illustrations of new taxa, ecological summaries and distribution maps. Five new species and several new subspecies are described.

MATERIAL AND METHODS

This revision is founded largely on my own field studies, collections and cultivated material, representative specimens of which are deposited at Reading University (RNG) and the British Museum (Natural History) (BM). Descriptions are based on both living and dried material and variation ranges attempt to cover the total variation encountered for a particular taxon. However, where abnormal values have been found these have usually been placed in parentheses either before or after the main ranges of variation. Flowering periods, chromosome numbers, ecological data, locality lists and distribution maps have all been compiled from specimens I have seen and only from literature references when substantiated with authentic material.

In addition to my own collections, specimens from the following herbaria have also been examined (abbreviations following Lanjouw & Stafleu, 1964) :

Botanisches Museum, Berlin-Dahlem, Germany (B).
British Museum (Natural History), London, England (BM).
Botanical Museum and Herbarium, Copenhagen, Denmark (C).
Botany School, University of Cambridge, England (CGE).
Herbarium Universitatis Florentinae, Firenze, Italy (FI).
Conservatoire et Jardin Botanique, Génève, Switzerland (G and G-DC).
Royal Botanic Gardens, Kew, England (K).
Rijksherbarium, Leiden, Netherlands (L).
The Linnean Society of London, England (LINN).
Botany Department, The University of Leicester, England (LTR).

Instituto 'Antonio José Cavanilles', Madrid, Spain (MA).
Museu Municipal do Funchal, Madeira (MADM).
University Herbarium, University of Michigan, Ann Arbor, Michigan, U.S.A. (MICH).
New York Botanical Garden, U.S.A. (NY).
Muséum National d'Histoire Naturelle, Paris, France (P).
Royal Horticultural Society, London, England (RHS).
Department of Botany, University of Reading, England (RNG).
Naturhistoriska Riksmuseum, Stockholm, Sweden (S).
Departamento de Botanica, Universidad de Sevilla, Spain (SEV).
School of Botany, Trinity College, Dublin, Ireland (TCD).
Jardín de Aclimatación de la Orotava, Tenerife (TENE).
Naturhistorisches Museum, Wien, Austria (W).
Botanischer Garten und Institut für Systematische Botanik der Universität Zürich, Switzerland (Z).

I have also had the opportunity to study living specimens collected by the late Dr E. R. Sventenius which are cultivated at the Tafira Botanic Garden, Gran Canaria, Spain.

HISTORICAL SURVEY

The following survey gives a chronological account of contributions to the knowledge of *Argyranthemum* and details of the various conflicting generic treatments applied to the species in critical revisions, floras and systematic surveys. The first account of an *Argyranthemum* species is found in Linnaeus's description of *Chrysanthemum frutescens* L. in his *Hortus Cliffortianus* (1738), although the first accurate record of this taxon is an illustration by Plukenet in his *Almagestum Botanicum* (1696). The second and only other species to be discovered in the 18th century, *Chrysanthemum pinnatifidum* L. f., was described by the younger Linnaeus in his *Supplementum Plantarum* (1781) from material collected by Masson on Madeira in 1778.

Linnaeus's (1737, 1753, 1754) concept of *Chrysanthemum* was an extremely wide one, embracing species now referable to the genera *Leucanthemum* Miller, *Dendranthema* Des Moul., *Chrysanthemum* L. sensu stricto, *Tanacetum* L. and *Matricaria* L. In efforts to improve the heterogeneous nature of this original generic concept, most post-Linnean syantherologists dealing with the Chrysantheminae Less. have invariably attempted to redefine generic limits. The treatments were quite often based entirely on one unreliable diagnostic character, and this has led to an extremely confused situation within the subtribe.

One of the first efforts was that of Zinn (1757), who reclassified species with white ligules, formerly placed in *Chrysanthemum*, into a new genus *Pyrethrum* Zinn. Species included in this new genus were equivalent to the Eurasian *Pyrethrum corymbosum* (L.) Scop. and the Macaronesian *P. frutescens* (L.) Gaertn. Sprague (1934) and Heywood (1954) have both established that *Pyrethrum* Zinn is the first nomenclaturally acceptable use of the generic name, although binomials were not used in the text. Heywood (1954) has also shown that the subsequent use of *Pyrethrum* during the latter part of the 18th century by authors such as Haller (1768), Scopoli (1772) and Gaertner (1791), invariably included *P. corymbosum* as a component species, whilst *P. frutescens* was occasionally left out. He concluded, therefore, that no matter what rank is acceptable for *Pyrethrum*, *P. corymbosum* must be chosen as the type.

In 1791 Desrousseaux amended the generic delimitations of the Chrysantheminae on the basis of pappus morphology. To illustrate the effect of this reshuffle, the Macaronesian taxa, *Pyrethrum frutescens* (L.) Scop. and *Chrysanthemum pinnatifidum* L. f. were both transferred to the newly defined genus, *Matricaria* L. The arrangement had a slight advantage over previous treatments in that the two closely related Macaronesian species were included in the same genus, separated from the heterogeneous *Chrysanthemum*, and removed from the inappropriate *Pyrethrum*. However, there was no real improvement on previous generic treatments as the separation was based on a single, unreliable diagnostic character :

'*Matricaria* – pappus marginatus,
Chrysanthemum – pappus nullus',

and both amended genera included heterogeneous groups of unrelated species, now referable to *Matricaria*, *Tanacetum*, *Chrysanthemum* and *Leucanthemum*.

At the turn of the 19th century, two new major surveys of the Chrysanthemineae appeared in the works of Smith (1800) and Willdenow (1803). Both authors adopted morphological criteria for generic delimitation similar to Desrousseaux's, but unsatisfactorily again used the name *Pyrethrum* instead of *Matricaria* for the species with a marginate pappus. The unreliability of the pappus character was immediately exposed when Willdenow separated the two species of *Argyranthemum* and placed them in different genera!

In 1801, Broussonet, who was at that time the governor of Tenerife, distributed seed material of many Canary Islands genera to the Berlin, Geneva and Leiden herbaria. From cultivated specimens derived from this seed material Persoon (1807) provided a description for a third species of *Argyranthemum*, the spectacular laurel forest species from northern Tenerife, '*Chrysanthemum broussonetii*', which he named in honour of the collector. Of plants grown from this original seed material, Willdenow (1809) described five new species from Tenerife, *Pyrethrum anethifolium*, *P. crithmifolium*, *P. foeniculaceum*, *P. coronopifolium* and *P. grandiflorum*. From examination of his type specimens it is now possible to refer the first three names to one species, *Argyranthemum foeniculaceum* (Willd.) Webb ex Schultz Bip., the fourth is the very rare and distinct species, *A. coronopifolium* (Willd.) Webb ex Schultz Bip., and the last one is conspecific with *A. frutescens* (L.) Webb ex Schultz Bip. subsp. *frutescens*.

One of the most important sources of distribution records for taxa of *Argyranthemum*, particularly on Tenerife, is L. von Buch's treatise, *Physicalische Beschreibung der Canarischen Inseln* (1825). In this work the conclusions of Link and Choisy, who independently examined all of von Buch's material are given, and it provides the earliest records of *Argyranthemum gracile* Schultz Bip. (*P. foeniculaceum* [var.]

bipinnatifidum Choisy) and the poorly known, narrow-leaved upland laurel forest taxon *Pyrethrum adauctum* Link (*Argyranthemum adauctum* subsp. *adauctum*).

Although by this time there had been considerable improvement in the knowledge of the Canary Islands flora, nothing had been done to improve the unreliable generic classification of the Chrysantheminae. Matters were greatly improved, however, when De Candolle (1838) provided multi-character diagnoses for different genera, whilst revising all known species in his monumental *Prodromus*. Here, *Chrysanthemum* remained small and was characterized by the presence of white or yellow ligules and heteromorphic cypselas. The genus, which was divided into a number of sections, contained all known species referable to *Argyranthemum*, five endemics of the South African Cape Province, one North African annual (*Chrysanthemum carinatum* Schousb.) and four European annuals (*C. coronarium* L., *C. segetum* L., *C. roxburghii* Desf. (= *C. coronarium*) and *C. viscosum Desf.* (= *C. viscido-hirtum* (Schott) Thell.)). Microfiche photographs of De Candolle's specimens show that the South African material lacked cypselas, but the taxa were presumably included in the genus *Chrysanthemum* by their superficial resemblance, i.e. their woody habit, to the Macaronesian species of the *Argyranthemum* group. My own unpublished studies of the African endemics have shown that the cypselas are homomorphic, 5–10 ribbed, and distinctly pappose, characters most resembling those of North African species of *Leucanthemum*.

De Candolle described no new Macaronesian taxa but did make several new combinations from taxa previously described by Willdenow (1809), and Link and Choisy (in L. von Buch, 1825).

The remainder of the Chrysantheminae were primarily separated from *Chrysanthemum* on the basis of their homomorphic cypselas. Unfortunately the treatment of the two larger genera, *Pyrethrum* and *Tanacetum*, was very unsatisfactory as it was influenced by the work of previous authors. The genera were kept distinct and separated from one another on unreliable floral characters such as discoid versus ligulate capitula.

A second woody perennial from Madeira, *Chrysanthemum dissectum*, was described by Lowe in 1838.

Probably the most important contribution to the taxonomy of the Macaronesian Chrysantheminae can be found in Webb & Berthelot's *Phytographia Canariensis* (1835–1850).

In 1839 and 1840 Webb and Berthelot published a series of seven plates of Canary Islands taxa, using the generic name *Argyranthemum* for the first time, but not giving it valid publication. Webb obviously thought that the Macaronesian species were quite distinct from all other genera in the Chrysantheminae but the plates give no indication of the characters he chose for separation. He applied a fairly wide species concept, and his plate of *Argyranthemum pinnatifidum* shows representatives of all the broad-leaved taxa with dentate secondary leaf lobes then known from the Canary Islands and Madeira, those now regarded as *A. dissectum*, *A. broussonetii* and *A. webbii*, all of which he regarded as conspecific with the Madeiran endemic to which the name he used applies. He also illustrated *A. frutescens*, with four varieties, *A. foeniculaceum* and *A. anethifolium*, presumably based on the *Chrysanthemum* species with those epithets, although he misinterpreted Willdenow's *Pyrethrum anethifolium* (= *Chrysanthemum anethifolium* (Willd.) Buch) and applied the name *Argyranthemum anethifolium* to an undescribed subalpine species named below *A. tenerifae* C. J. Humphries. There were also plates of two species from Webb's own collections made in the late 1820's that he thought were new, *A. jacobaeifolium* (*A. adauctum* subsp. *jacobaeifolium* (Webb ex Schultz Bip.) C. J. Humphries) from Gran Canaria, and *A. ochroleucum* (= *A. maderense* (D. Don) C. J. Humphries) from Lanzarote.

The account of the Compositae in the text of the *Phytographia Canariensis* was written by Schultz Bipontinus and published in 1844 (Stearn, 1937). Along with his studies on European Chrysantheminae, Schultz Bipontinus (1844b), by using cypsela morphology, provided a set of truly reliable characters on which to rest a generic classification. Perhaps the most significant point to emerge from his work was that no real differences could be found between *Pyrethrum* and *Tanacetum*. He transferred many species into the latter genus as it had nomenclatural priority.

Schultz Bipontinus was over-zealous in his application of cypsela characters to the Macaronesian taxa. Species referable to *Argyranthemum* were placed into five smaller genera, *Argyranthemum* Webb ex Schultz Bip., validly published in this account, *Preauxia* Schultz Bip., *Monoptera* Schultz Bip., *Stigmatotheca* Schultz Bip. and *Ismelia* Cass., with little regard for the overall morphological unity in the group. His diagnostic characters, however, are still of considerable value for separating five distinct species groups within *Argyranthemum* and are thus used as sectional criteria in this revision. He postulated a morphological link with the annual Mediterranean species of *Chrysanthemum* on the basis of the 'smooth' or 'ribless' cypselas, by including the North African *Chrysanthemum carinatum* and the two Canarian endemics, *A. broussonetii* and *A. coronopifolium*, in the genus *Ismelia* Cass.

Briefly summarizing, we see for the first time some fairly reliable data on which the generic classification in the Chrysanthemum complex can be based, although admittedly there was some unnecessary splitting for the Macaronesian species. The view that these taxa do form a unique morphological group was endorsed by Lowe (1868) when he included the three woody endemic species of Madeira, *Argyranthemum pinnatifidum*, *A. dissectum* and *A. haemotomma*, in the same genus. Apart from their woody habit, he considered that the nature of the convex conical receptacle also supported a separation from *Chrysanthemum*.

Despite the valuable technical basis for generic classification in the Chrysantheminae devised by Schultz Bipontinus, cypsela characters were largely ignored by writers in the latter half of the 19th century, as reliance on them alone gave inconsistent treatments in different groups. Bentham (1873), for example, reverted to an unsatisfactory arrangement by using floret characters in which *Chrysanthemum* remained distinct from *Tanacetum* but contained *Argyranthemum* and *Pyrethrum* as component sections. Hoffman (1889–1894) improved matters slightly by uniting *Tanacetum* with *Pyrethrum*, but also united *Argyranthemum* with the unrelated east European group, *Bracanthemum* DC., and kept it as one of the component sections of a large heterogeneous genus, *Chrysanthemum*, along with species of *Leucanthemum*, *Tanacetum* and *Pyrethrum*.

By the turn of the present century, there were three points of view on the treatment of *Argyranthemum*. The first one accepted Schultz Bipontinus's split of the group into a number of small genera, as endorsed by Pitard & Proust (1908 : 226–233) in an account of some new records for the Canary Islands. The second view was briefly hinted at by Webb in 1839 and 1840 (Webb & Berthelot, 1836–1850) and Lowe (1868), who accepted that the species of *Argyranthemum* were distinct and formed a single homogeneous grouping endemic to the Macaronesian region. The third, more generally accepted, view, which regarded *Argyranthemum* as a component section of *Chrysanthemum*, has prevailed until the present day (Larsen, 1958, 1960 ; Sventenius, 1960 ; Lid, 1967 ; Borgen, 1969, 1970, 1971, 1972).

During this century the generic boundaries in the Chrysantheminae have been re-examined by a number of botanists using the new systematic techniques now available : embryology, phytochemistry, cytology and cypsela anatomy. For the most part this work has been based primarily on European and Oriental taxa but as the summary given below will show it is relevant to the problem of the position and limits of *Argyranthemum*.

In 1916, Briquet and Cavillier published a new classification of the Chrysantheminae for E. Burnat's *Flore des Alpes Maritimes*. In this work, three main genera were recognized on the basis of a detailed morphological and anatomical study of fruit structure. The synthesis separated *Leucanthemum* Miller, *Tanacetum* L. and *Chrysanthemum* L. on the heteromorphic versus homomorphic nature of the cypselas and by the presence or absence of pericarp modifications such as secretory myxogenic cells, mesocarp secretory lacunae and vallecular canals. Briquet's results endorsed the earlier conclusion of Schultz Bipontinus that an association of *Pyrethrum* with *Chrysanthemum*, distinct from *Tanacetum*, was wholly unacceptable. Possibly because the *Flore des Alpes Maritimes* was no more than a regional flora, and the basis for the generic limits adopted in it was not argued at any great length, few systematists have taken up Briquet's and Cavillier's ideas and most have taken up broader, less satisfactory classifications. When anatomical studies have been applied to other floras the results have usually supported Briquet's system. Thus, Giroux (1930, 1933) provided a wealth of data for the Chrysantheminae of North Africa. Horvatić (1935, 1963) has also shown that the criteria hold good for most species in *Leucanthemum*. However, the carpological distinctions between *Tanacetum* and *Leucanthemum* are not particularly clear when applied to critical species, as shown by Heywood (1954) in his account of the Spanish taxa of *Tanacetum* sect. *Pyrethrum* subsect. *Leucanthemopsis* (Giroux) Heywood. Similarly the status of various other groups closely related to *Tanacetum*, *Chrysanthemum* and *Leucanthemum*, such as *Argyranthemum* and lesser known genera, *Hymenostemma* (Kunze) Willk., *Plagius* L'Hér. ex DC. and *Coleostephus* Cass., is difficult to interpret on anatomical criteria alone (Humphries, 1973).

In 1951, Harling provided an extensive treatise on the embryology of the Chrysantheminae and the systematic conclusions derived from this work generally support Briquet's system of classification. In the Chrysanthemum complex mono-, bi- and tetrasporic embryo-sac developments have all been observed. The genera *Chrysanthemum* and *Leucanthemum* are monosporic, all species of *Tanacetum* are tetrasporic and *Argyranthemum* has a unique bisporic embryo-sac development. Recent studies on *Argyranthemum* and *Tanacetum* sect. *Fruticosa* by Borgen (1971, 1972) confirm the original observations made by Harling, which suggest that *Argyranthemum* is independent of the rest of the Chrysantheminae.

Cytological information has proved to be of little taxonomic use except for studying species relationships within polyploid genera such as *Leucanthemum* and *Dendranthema* (Favarger, 1959; Favarger & Villard, 1965; Polatschek, 1966; Villard, 1970; Shimotomai *et al.*, 1939, 1956, 1957, 1958, 1960; Tanaka, 1959a, b, c). The basic number of the Chrysantheminae is $x = 9$ and the somatic number ranges from $2n = 18$ to $2n = 198$ (Dowrick, 1952). *Argyranthemum* species are all diploid ($2n = 18$) (Larsen, 1960; Borgen, 1969, 1970) with little apparent variation in the karyotype (Humphries, 1973).

Over the last ten years there have been a few papers devoted to the systematic comparison of phytochemical characters within the Chrysantheminae. Bohlman *et al.* (1964), for example, showed that different classes of leaf polyacetylenes closely follow the groupings derived from cypsela studies. Favarger (1966) observed the presence of an anthocyanin pigment in root tips of species in the genus *Leucanthemum*. Finally, Harborne *et al.* (1970) have very recently shown that the reticulate flavonoid distribution within the Chrysanthemum complex fits very closely to Briquet's highly original scheme based on cypsela morphology and anatomy.

THE TAXONOMIC POSITION OF *ARGYRANTHEMUM*

The Anthemideae Cass. ex DC. are a well-defined tribe of the Compositae best characterized by the occurrence of scarious or papery receptacular bracts (phyllaries), a coriaceous or scarious coronal pappus, which is sometimes reduced to an apical aculus or is completely absent, truncate-penicilliate style tips, and strongly aromatic florets and leaves (after Cassini, 1829 : 403).

The tribe is usually divided into two subtribes; the Anthemidinae Dumort. and the Chrysantheminae Less. The Anthemidinae normally have chaffy scarious receptacular scales, invariably subtending the ovary and tubular part of the ray corollas and some, if not all, of the disc florets. Lessing (1831 : 167) considered the Chrysantheminae to be distinct from the Anthemidinae by the presence of naked receptacles, lacking receptacular scales. The division of the subtribes on this basis has recently been shown to be somewhat artificial when Greuter (1968) indicated that certain Cretan species of the genus *Ammanthus* Boiss. contain characteristics of both subtribes. It is inappropriate in this paper to become involved in a detailed discussion of the subtribal classification of the Anthemideae, as all taxa in the Chrysanthemum complex referable to the genus *Argyranthemum* lack receptacular scales and do not have any parallel genera in the subtribe Anthemidinae.

As already indicated in the historical review, generic relationships within the Chrysantheminae are far from being clear, although it is now more easily possible to discern clusters of species which have several distinguishing morphological and anatomical characters and a characteristic geographical distribution (Table 1).

TABLE I

Morphological characters used for generic delimitation in, and geographical distribution of the genera in the Chrysanthemum complex

	Habit			Leaves						Florets		Receptacle		Cypselas							Embryo-sac			
	annual	woody perennial	herbaceous perennial	opposite	alternate	toothed–entire	dissected	tomentose	glandular	fertile	sterile	plano-convex	convex–conical	homomorphic	heteromorphic	myxogenic cells	basal callus	resin canals	non-secretory canals	pappus present	monosporic	bisporic	tetrasporic	Geographical distribution
Argyranthemum Webb ex Schultz Bip.	–	+	–	–	+	–	+	[+]	[+]	+	–	–	+	–	+	–	–	–	–	[+]	–	+	–	Macaronesia
Chrysanthemum L.	+	–	–	–	+	[+]	[+]	–	–	+	[+]	–	+	–	+	–	–	–	–	+	+	–	–	Mediterranean region
Pinardia Cass.	+	–	–	–	+	–	+	–	+	+	–	–	+	+	–	–	–	–	–	+	–	–	+	S.W. Asia–N. Africa
Leucanthemum Miller	–	–	+	–	+	[+]	[+]	–	–	+	–	–	+	+	–	+	–	+	+	+	+	–	–	Europe–N. Africa
Coleostephus Cass.	+	–	–	–	+	+	–	[+]	–	+	+	+	–	+	–	+	+	+	+	+	+	–	–	Europe
Glossopappus Kunze	+	–	–	–	+	+	–	[+]	–	+	+	–	+	+	–	+	+	+	+	+	+	–	–	Europe
Plagius L'Hérit. ex DC.	–	–	+	–	+	+	–	–	–	+	–	–	+	+	–	+	+	+	+	+	+	–	–	Europe
Tanacetum L.	–	[+]	[+]	–	+	–	+	[+]	[+]	+	–	–	+	+	–	[+]	–	–	–	–	–	–	+	N. hemisphere
Leucanthemella Tzvelev	–	–	+	–	+	–	+	+	–	–	+	–	+	+	–	–	–	–	+	+	?	?	?	Russian Asia
Hymenostemma (Kunze) Willk.	+	–	–	–	+	–	+	+	–	–	+	–	+	+	–	+	–	–	–	+	?	?	?	Europe
Hippolytia Pojark	–	–	+	–	+	–	+	+	+	+	–	–	+	+	–	–	–	–	–	–	?	?	?	Russian Asia
Balsamita Miller	–	–	+	–	+	+	–	+	+	+	–	–	+	+	–	–	–	–	–	+	–	–	+	S.W. Asia–Europe
Prolongoa Boiss.	+	–	–	+	–	–	+	+	–	–	+	–	+	+	–	+	–	–	–	+	?	?	?	Europe
Phalacrocarpon Willk.	–	+	–	+	–	–	+	+	–	+	–	–	+	+	–	–	–	–	–	–	?	?	?	Europe
Dendranthema (DC.) Des Moul.	–	+	–	–	+	[+]	[+]	+	[+]	+	–	–	+	+	–	[+]	–	–	–	–	+	–	–	Oriental Asia

Thus, on the basis of differences in habit, cypsela morphology, cypsela anatomy and embryo-sac development, most of the species of the Chrysanthemum complex can be referred to one of five main genera ; *Tanacetum* L., *Chrysanthemum* L. sensu stricto, *Leucanthemum* Miller, *Dendranthema* (DC.) Des Moul. and *Argyranthemum* Webb ex Schultz Bip. Around these genera one finds a number of species which do not fit into the main groups and should be placed in independent satellite genera. Amongst these are *Plagius* L'Hérit. ex DC., *Hymenostemma* (G. Kuntze) Willk., and *Coleostephus* Cass., closely allied to *Leucanthemum* ; *Hippolytia* Pojark, *Balsamita* Miller and *Leucanthemella* Tzvelev, morphologically similar to *Tanacetum* L. ; and *Pinardia* (Cass.) DC. (to include *Chrysanthemum viscido-hirtum* (Schott) Thell.), very close to the genus *Chrysanthemum*.

The transitions between different genera are very rarely clearly worked out. One of the few groups to be studied in detail is the species group of *Tanacetum* sect. *Pyrethrum* subsect. *Leucanthemopsis* (Giroux) Heywood, in which Harling (1951) and Heywood (1954) show that a transition between *Tanacetum* and *Leucanthemum* occurs in Europe, particularly in plants from the Iberian peninsula.

Argyranthemum most closely resembles *Chrysanthemum* L. sensu stricto and its satellite genus *Pinardia* Cass. The three genera can readily be distinguished from all other taxa in the Chrysantheminae by the possession of heteromorphic (versus homomorphic) cypselas. Also, several other characters which vary in a reticulate fashion in the Chrysanthemum complex, such as the annual or perennial habit, leaf dissection, receptacle shape, cypsela anatomy and embryo-sac development, serve independently to separate *Argyranthemum*, *Chrysanthemum* and *Pinardia* from other genera when used in combination with the heteromorphic cypsela character (Table 1). Further discussion on generic treatments in homomorphic-fruited taxa can be found in the works of Briquet & Cavillier (1916), Tzvelev (1961), Harling (1951), Heywood (1954), Favarger (1966), Jeffrey (1971), and will not be considered in this paper.

In the narrowest sense *Chrysanthemum* contains three annual species, *C. segetum* L., *C. coronarium* L. and *C. carinatum* Schousb., predominantly distributed around the European Mediterranean region, S.W. Asia and N. Africa. The original distribution of the first two species, *C. segetum* and *C. coronarium*, is difficult to establish with certainty however, as they are now found as weeds in most temperate regions of the world.

The genus *Chrysanthemum* can be divided into two sections. Section *Chrysanthemum* contains the two weedy species, *C. segetum* and *C. coronarum*, and is characterized by the presence of yellow florets, secretory lobes on the corolla lobes of the disc florets, and epappose and wingless disc cypselas with 5–10 regularly spaced ribs. The second section, *Ismelia* (Cass.) DC., containing *C. carinatum*, has purple disc florets, red-purple, white and yellow ray florets, unribbed or irregularly ribbed and biwinged disc cypselas with a coroniform pappus. Plants of both sections are glabrous and have a monosporic embryo-sac development (Harling, 1951).

The monotypic genus, *Pinardia* (Cass.) DC., containing *P. viscido-hirtum* Schott, is usually included as a component section of the genus *Chrysanthemum*. It diverges, however, in having viscous glandular hairs on all vegetative parts, cypselas with apical aculei and a tetrasporic embryo-sac development (Harling, 1951).

C. carinatum is undoubtedly the closest extra-Macaronesian species to the genus *Argyranthemum* and on the basis of cypsela morphology is most similar to the large-flowered species of *A.* sect. *Sphenismelia* (Schultz Bip.) C. J. Humphries. The natural distribution of *C. carinatum* in North Africa and the Salvage Islands, thus, provides a phytogeographical as well as a morphological link between the Mediterranean and Macaronesian genera.

Despite the obvious transitions which do exist between the two genera, all species of *Argyranthemum* can consistently be separated from species of *Chrysanthemum* by their woody, perennial habit, and the unique bisporic embryo-sac development (Harling, 1951 ; Borgen, 1972). Recently various phytochemical differences of both the leaves and florets have also been found (Bohlman *et al.* 1964 ; Humphries, 1973). Both morphological characters and geographical distribution indicate that this group of species is a well-delimited and natural one, and species of *Argyranthemum* can be separated from others in the Chrysanthemum complex as consistently as those in other segregate genera of the Anthemideae recently recognized (Briquet & Cavillier, 1916 ; Heywood, 1954, 1958b ; Tzvelev, 1961 ; Favarger, 1966).

MORPHOLOGICAL CHARACTERS

Habit and Growth Form

Many of the endemic genera of the Macaronesian region, and particularly the Canary Islands, contain a high percentage of woody perennials (Lems, 1960). All species of *Argyranthemum* develop woody stems in the first year of growth, being gnarled and frequently ridged towards the base. The degree of woodiness is extremely variable, ranging from a slight thickening at the base of a slender herbaceous stem (e.g. *A. gracile* and *A. filifolium*) to a more or less completely woody trunk in the forest species (e.g. *A. broussonetii* and *A. haouarytheum*).

The habit and branching pattern are closely related to different ecological conditions. North coast chasmophytes of Tenerife and Gran Canaria (e.g. *A. coronopifolium* and *A. frutescens* subsp. *canariae*), for example, develop as low-growing decumbent shrubs, with short, stout fleshy stems, in response to the prevailing wet oceanic northerly winds. Plants with reduced seasonal cycles such as xerophytes of sub-alpine and arid south-facing slopes of Tenerife, Gran Canaria and La Gomera tend to have reduced lignification and develop either as dome-shaped plants branched almost entirely from the base, e.g. *A. tenerifae* and *A. adauctum* subsp. *gracile*, or as slender short-lived perennials, e.g. *A. gracile* and *A. filifolium* (Fig. 1). Inland cliff chasmophytes (e.g. *A. pinnatifidum* and *A. foeniculaceum*) develop a distinct candelabra-like branching pattern which is commonly found in other Macaronesian endemic genera such as *Echium* (Boraginaceae) (Bramwell, 1972) and *Aeonium* (Crassulaceae) (Lems, 1960). The branches diverge from all parts of the main stem at an angle between 45 ° and 90 °, eventually becoming ascending. The capitula develop singly at the tips of the peduncles at more or less the same height (*A. foeniculaceum*), or as lax, globose corymbs (*A. pinnatifidum*). The lower leaves are caducous, and owing to the short internodes the upper leaves are crowded around the peduncles (Fig. 1).

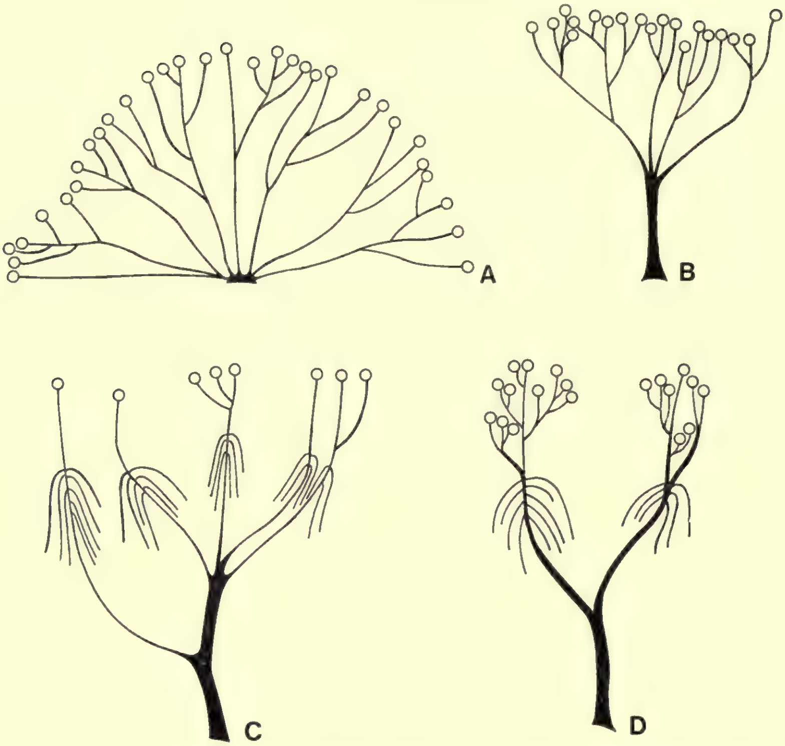

Fig 1. Branching patterns in *Argyranthemum* : A, *A. tenerifae*, *A. adauctum* subsp. *gracile* ; B, *A. gracile*, *A. filifolium* ; C, *A. foeniculaceum* ; D, *A. pinnatifidum*.

The largest plants of the genus are found in sheltered habitats with high rainfall, such as the laurel and pine forests of the western Canary Islands. In Tenerife, individuals of *A. broussonetii* are frequently up to 3 or 4 metres in diameter and well over 1 m in height.

Leaves

The leaves are alternate and are usually differentiated into lamina and petiole, although the latter is absent or reduced in sect. *Preauxia* and *Stigmatotheca*, and in some populations of *A. broussonetii* (Fig. 2N, R, V). The leaves are variously dissected, being sub-entire or with dentate margins (e.g. *A. pinnatifidum*, Fig. 2R), pinnatilobed or bipinnatilobed (e.g. *A. coronopifolium*, *A. maderense*, Fig. 2M, G), pinnatifid or bi-pinnatisect (e.g. *A. adauctum* subsp. *gracile* and *A. foeniculaceum*, Fig. 2V2, D). Many of the differences in outline and dissection are taxonomically useful. For the purpose of description, the main lobes from the rachis are called primary lobes. The primary lobes may be well-defined paired obovate or ovate limbs, with smaller tooth-like secondary lobes (e.g. *A. adauctum*, *A. webbii*, *A. broussonetii*, Fig. 2U, P, N) or the primary and secondary lobes may be of almost

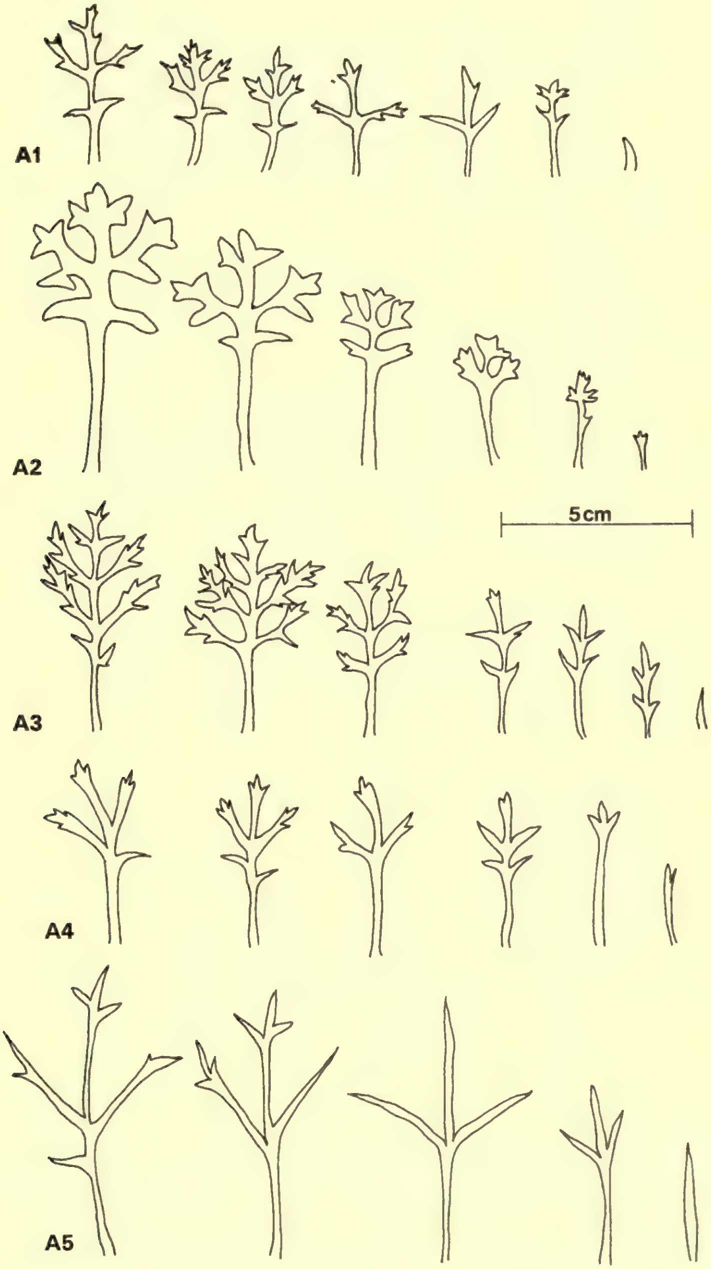

FIG. 2. Leaf morphology in *Argyranthemum* : A 1, *A. frutescens* subsp. *frutescens* ; A 2, *A. frutescens* subsp. *succulentum* ; A 3, *A. frutescens* subsp. *gracilescens* ; A 4, *A. frutescens* subsp. *parviflorum* ; A 5, *A. frutescens* subsp. *foeniculaceum*.

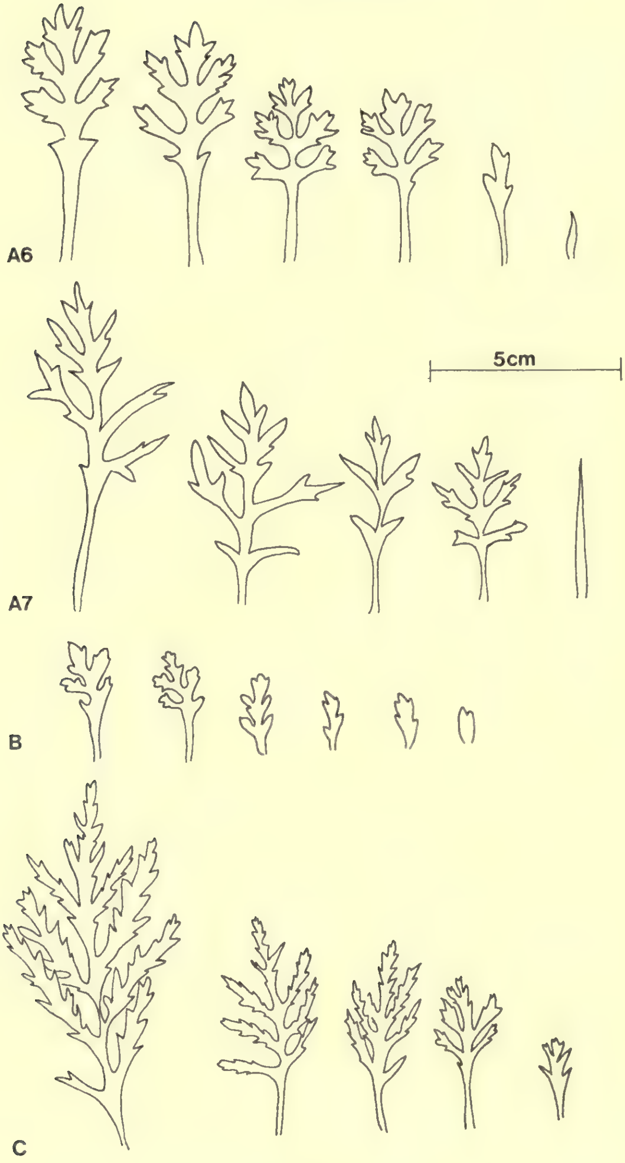

Fig. 2 (cont'd). Leaf morphology in *Argyranthemum* : A 6, *A. frutescens* subsp. *canariae* ; A 7, *A. frutescens* subsp. *pumilum* ; B, *A. lemsii* ; C, *A. haouarytheum*.

equal dimensions (e.g. *A. filifolium*, *A. foeniculaceum*, Fig. 2S, D). The number of leaf-lobes is normally very variable (e.g. *A. frutescens*) and is of little taxonomic use, although *A. gracile* invariably has trisect leaves (Fig. 2E). There is wide variation in absolute leaf size, from the short, narrow leaves of *A. lemsii* (Fig. 2B) to the extremely long, wide leaves of *A. broussonetii* and *A. pinnatifidum* (Fig. 2N, R).

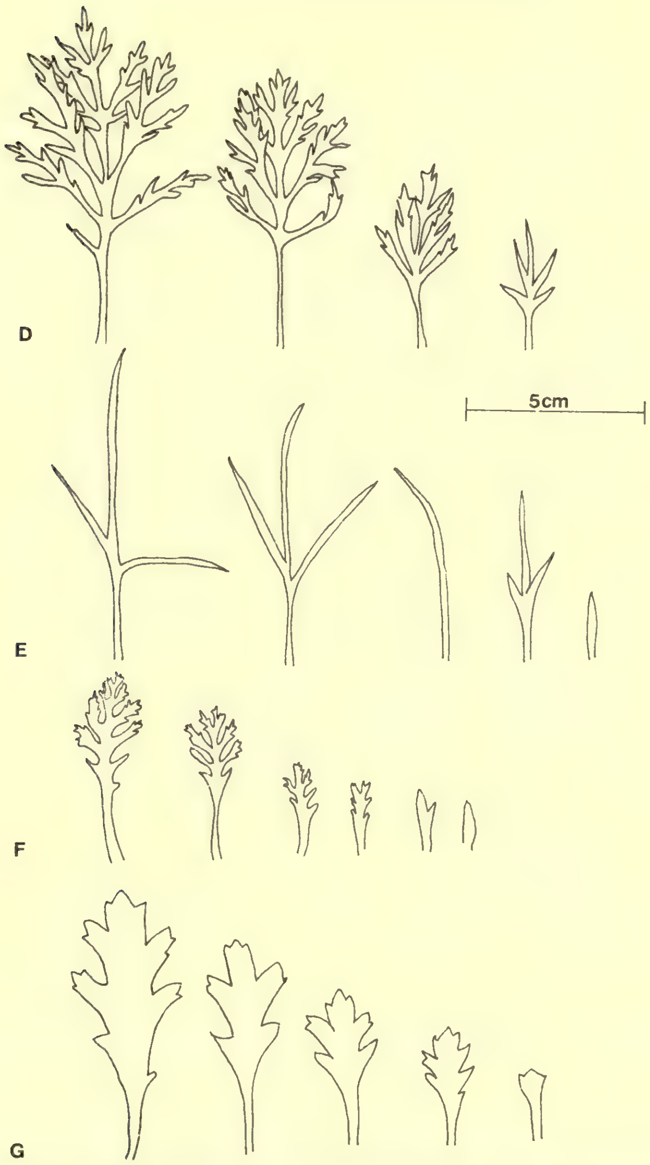

FIG. 2 (cont'd). Leaf morphology in *Argyranthemum* : D, *A. foeniculaceum* ; E, *A. gracile* ; F, *A. tenerifae* ; G, *A. maderense.*

Leaf characters provide the best examples of conspicuous responses to natural selection. Thus, in the widespread species *A. frutescens*, *A. adauctum* and *A. pinnatifidum* there is considerable variation in the dissection of the leaves, which is related to habitat and climate. The differences are maintained in cultivation and are rarely, if ever, due to environmentally induced plasticity (Fig. 2A, V). Leaves

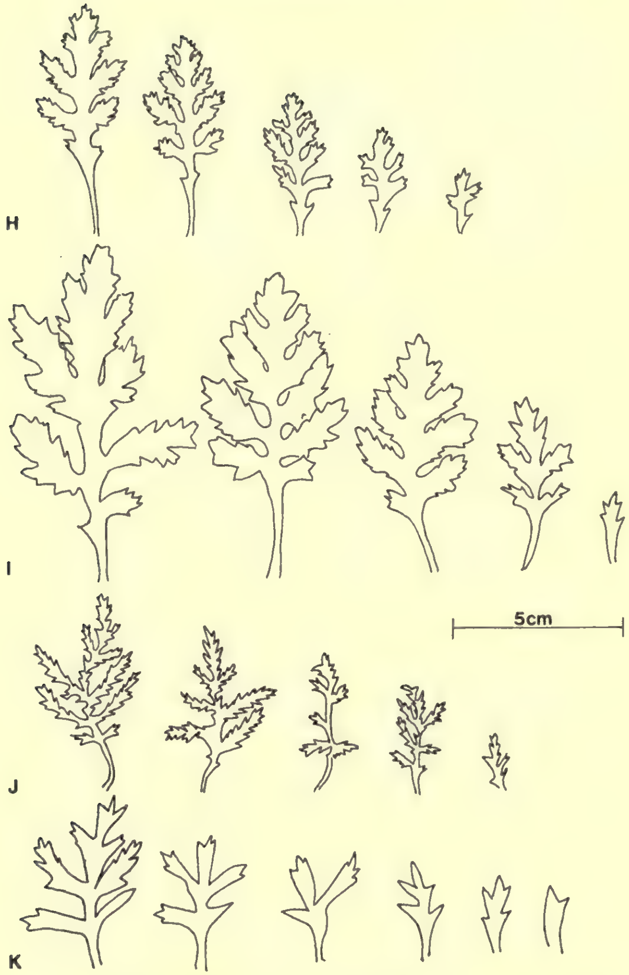

FIG. 2 (cont'd) Leaf morphology in *Argyranthemum* : H, *A. winteri* ; I, *A. lidii* ; J, *A. dissectum* ; K, *A. thalassophilum*.

of *A. frutescens* from the north coasts of Tenerife and Gran Canaria have broad, obtuse, fleshy lobes. Plants of xeric habitats on the south coast of Tenerife and the south-east and north coasts of Gomera have slender leaves with many narrow, acute leaf-lobes. Similarly, so do the forest populations of *A. adauctum*, particularly from north-facing slopes and alpine habitats. In *A. pinnatifidum* subsp. *succulentum* the fleshy texture of coastal populations increases with salinity ; the shortest, most succulent-leaved, individuals grow permanently in the spray zone along the coast (Fig. 2R2). As there is obviously a limited repertoire of leaf shape in the genus there is clearly convergence in morphology in particular environments. Thus, in the arid environments of the southern slopes of Gran Canaria and Tenerife, the

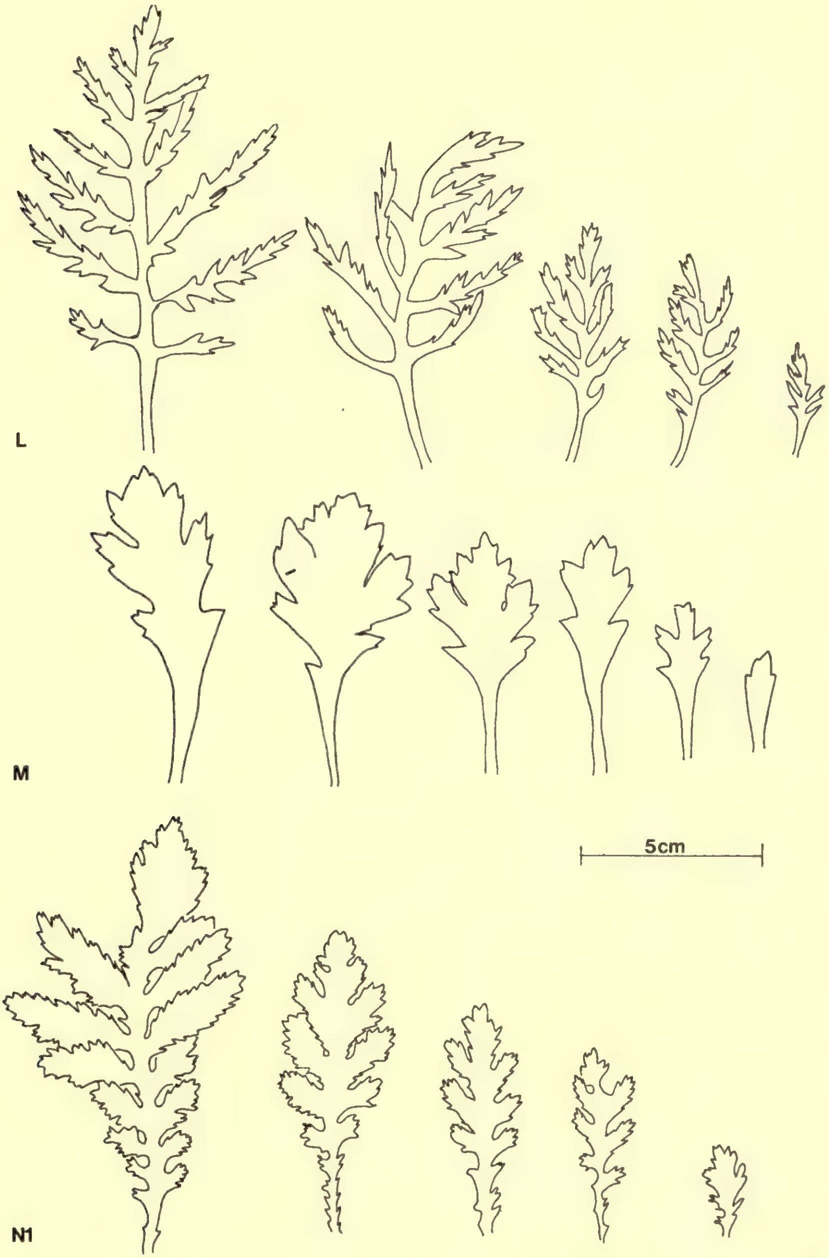

FIG. 2 (cont'd) Leaf morphology in *Argyranthemum* : L, *A. callichrysum* ; M, *A. coronopifolium* ; N 1, *A. broussonetii* subsp. *broussonetii*.

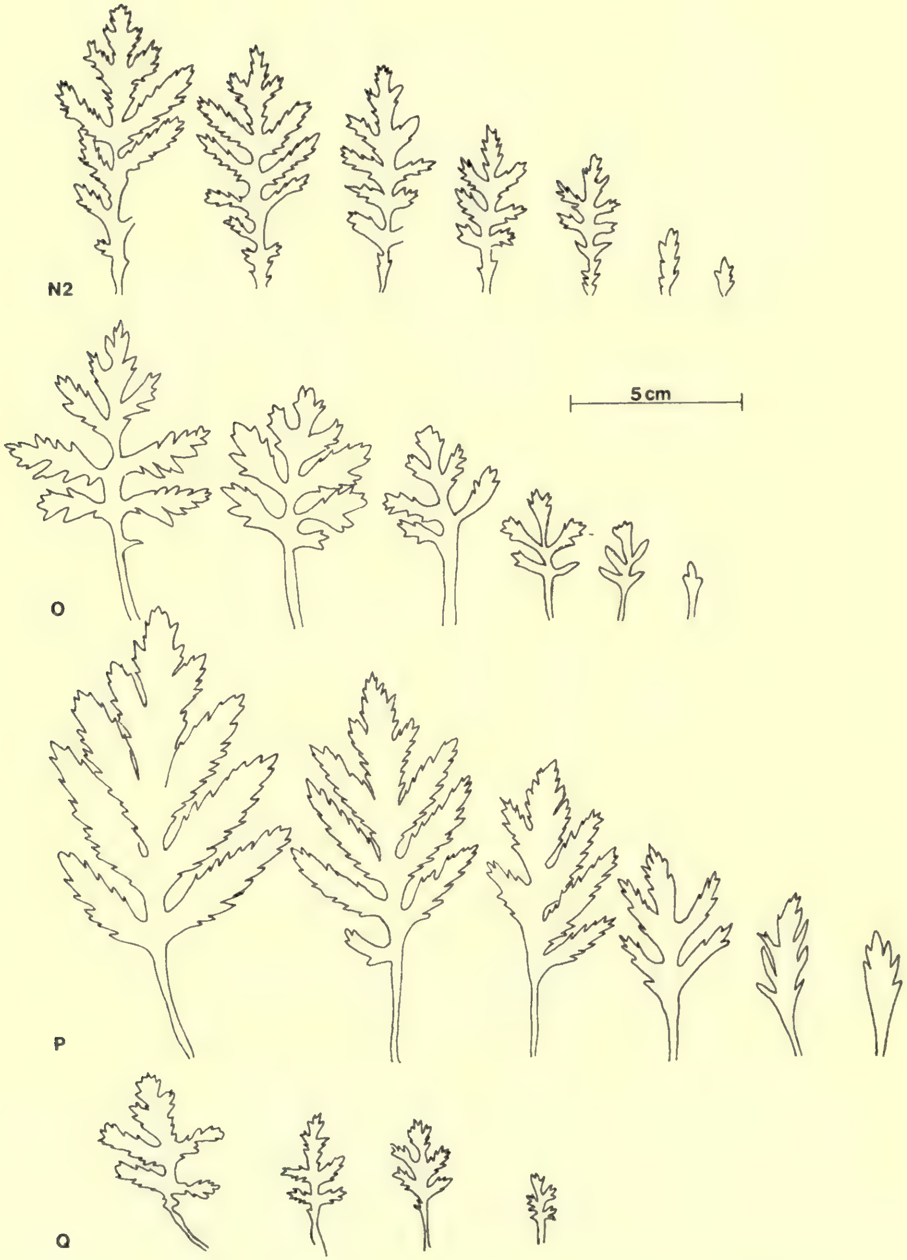

Fig. 2 (cont'd). Leaf morphology in *Argyranthemum*: N 2, *A. broussonetii* subsp. *gomerensis*; O, *A. hierrense*; P, *A. webbii*; Q, *A. haemotomma*.

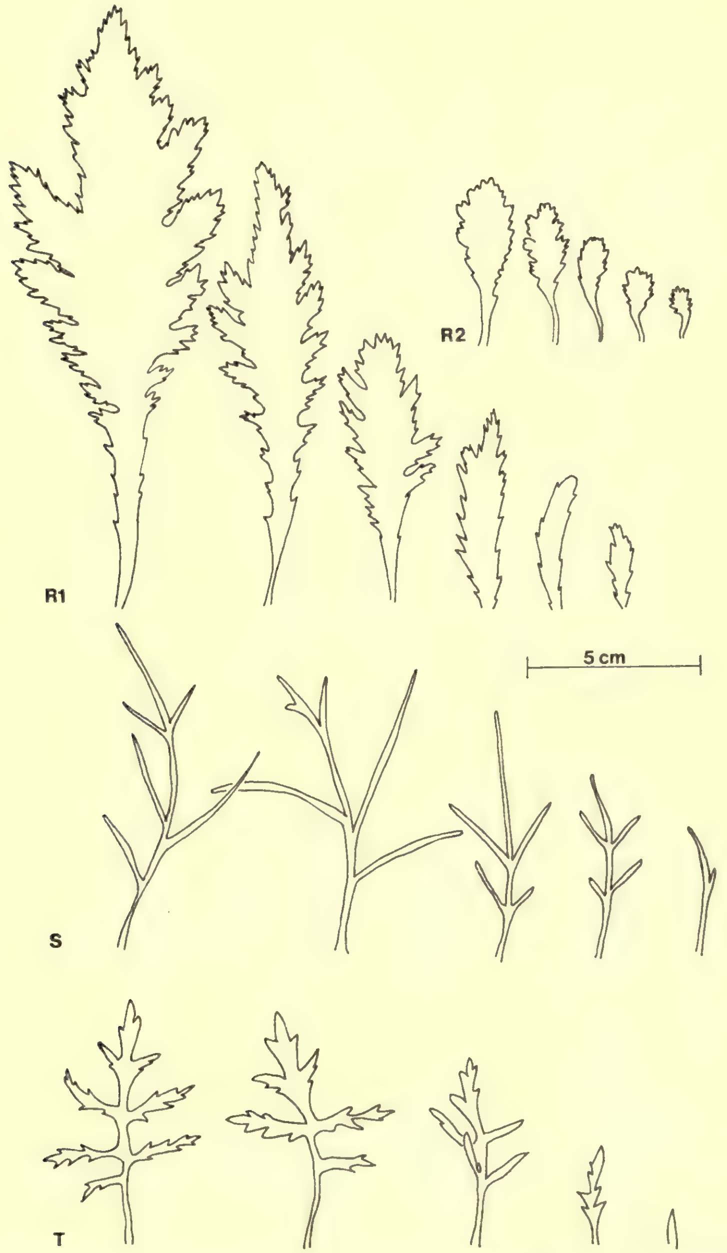

Fig. 2 (cont'd). Leaf morphology in *Argyranthemum*: R 1, *A. pinnatifidum* subsp. *pinnatifidum*; R 2, *A. pinnatifidum* subsp. *succulentum*; S, *A. filifolium*; T, *A. escarrei*.

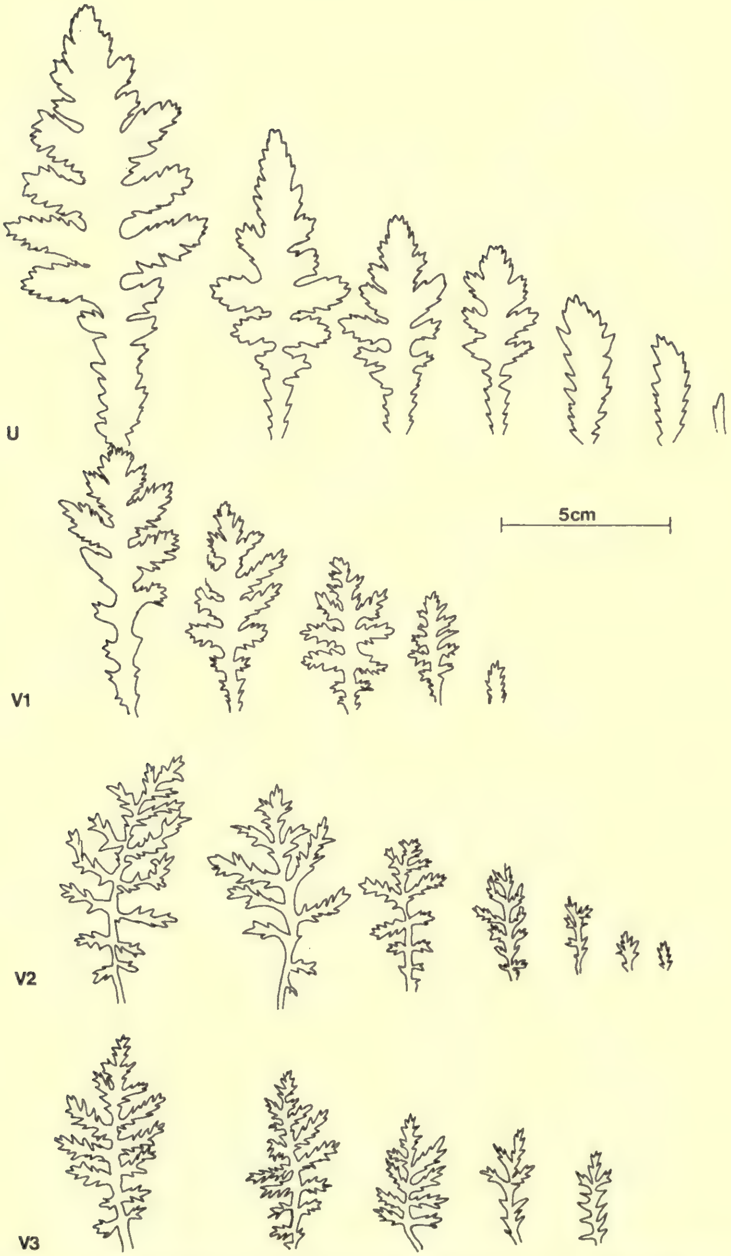

FIG. 2 (cont'd). Leaf morphology in *Argyranthemum* : U, *A. adauctum* subsp. *jacobaeifolium* ; V 1, *A. adauctum* subsp. *canariense* ; V 2, *A. adauctum* subsp. *gracile* ; V 3, *A. adauctum* subsp. *dugourii*.

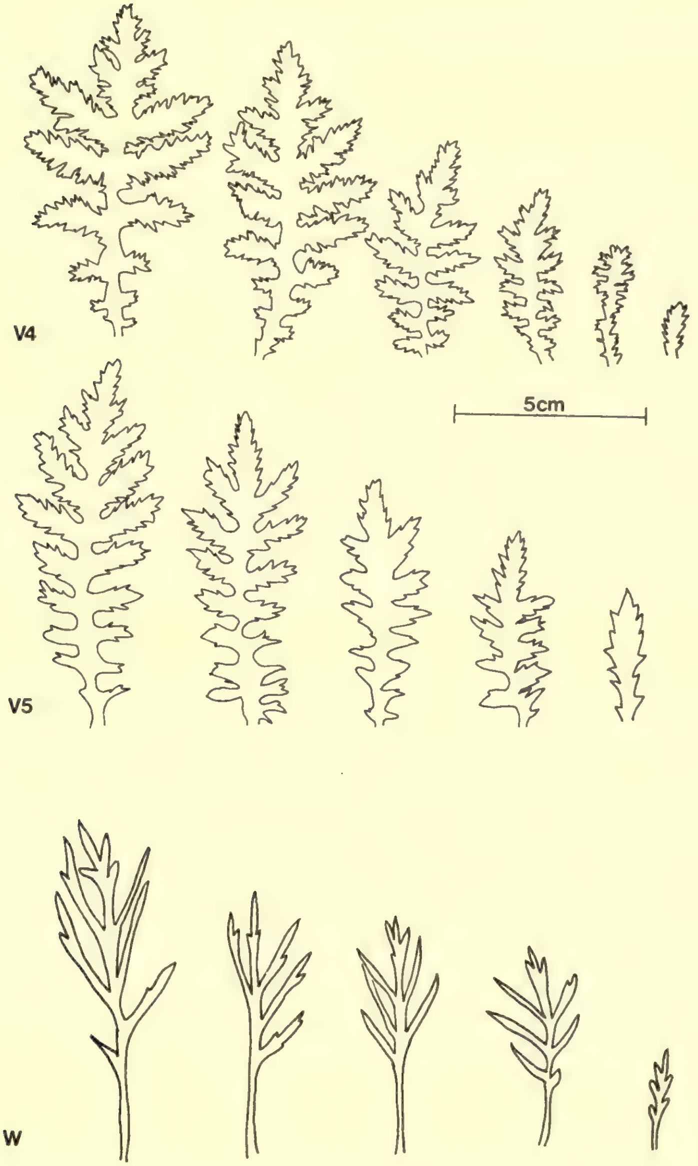

FIG. 2 (cont'd). Leaf morphology in *Argyranthemum* : V 4, *A. adauctum* subsp. *adauctum* ; V 5, *A. adauctum* subsp. *erythrocarpon* ; W, *A. sventenii*.

leaves of *A. filifolium* and *A. gracile* resemble other microphyllous plants common to the region. They are extremely dissected with a low number of leaf-lobes (Fig. 2E, R, S). Similarly coastal populations of *A. pinnatifidum* subsp. *succulentum*, *A. frutescens* subsp. *canariae* and subsp. *succulentum*, *A. thallassophilum* and *A.*

coronopifolium all show similar increased leaf succulence in response to the stringent conditions in the coastal communities in which they grow.

Indumentum

Most species of *Argyranthemum* are glabrous or sparsely pubescent on the stems and midrib. Conspicuously pubescent plants are only found in some populations of *A. adauctum*. The trichomes consist of two types. The most conspicuous are typically multicellular, unbranched hairs, with an enlarged terminal cell. The second type are small, rounded glandular hairs found predominantly on the lower leaf surface (Plate 28).

Inflorescence

The number of capitula in an inflorescence varies from one (as in some plants of *A. foeniculaceum*) to 30–50 (e.g. *A. hierrense* and *A. gracile*). A terminal capitulum develops first in the early stages of the inflorescence formation, followed by irregular alternate branching from lower bracts. The shape varies from a globose few-headed inflorescence with relatively short peduncles (e.g. *A. callichrysum*) to a lax open corymb with long peduncles (e.g. *A. gracile* and *A. filifolium*).

Capitulum

The shape of the capitulum is broadly to narrowly hemispherical and its size is extremely variable in species of wide ecological tolerance (e.g. *A. frutescens*, *A. pinnatifidum* and *A. broussonetii*). The size is normally quite uniform for any one population but frequently differs between them when they are completely separated. This suggests that it is controlled genetically, and the differences are apparently maintained by the lack of outcrossing between isolated populations (Humphries, 1973). Natural F_1 hybrids between the relatively small-headed *A. frutescens* and the large-headed *A. coronopifolium* have capitula of intermediate size while in the F_2 there is segregation to include sizes encountered in the species.

There is a wide range of variation in absolute capitulum size between different species, from the extremely narrow capitula in *A. filifolium* and Gomeran populations of *A. frutescens* to the broad capitula of *A. pinnatifidum*, *A. haemotomma* and *A. broussonetii*. Measurements are given in the descriptions.

Involucral Bracts

In all species the involucral bracts are imbricate and in 3–4 series. Bracts of the outer series typically have a triangular outline, with a thick fleshy midrib and thin scarious margins. The midrib of the outer bracts of *A. thallassophilum* is expanded into a broad fleshy keel. Bracts of the inner series vary from being linear-lanceolate to obovate or obspathulate in outline. The apex is usually expanded into a scarious lobe and is frequently laciniate or sinuate. Veins are conspicuously flabelliform at the apex in *A. thallassophilum* and easily observed in most species of section *Argyranthemum*. Bracts of *A. tenerifae* are distinctly narrow triangular in outline, with thin scarious margins, and expanded only slightly at the apex on the inner bracts.

In section *Preauxia* and in *A. tenerifae* (sect. *Argyranthemum*) the bracts are laxly imbricate in bud and can easily be removed, but in all other species they are tightly overlapping and difficult to remove.

Florets

All *Argyranthemum* species have conspicuously radiate capitula. Ray florets are female and the ligules are more or less linear-ovate in shape. The size and shape vary from the short, narrow ligules of *A. filifolium* to the long, broad ligules of *A. broussonetii* and *A. haouarytheum.* Measurements are given in the descriptions. The apex of the ligule can be entire, emarginate or 2- to 3-fid. They are normally white, but in *A. maderense* and *A. callichrysum* they are canary yellow, while in *A. haemotomma* they are white, pink or reddish-pink. The genetic basis of colour variation in *A. haemotomma* is unknown. The shade or colour tends to be constant for each population, but distinct between neighbouring populations, producing a wide range of colour variants within the species.

The disc florets are hermaphrodite and tubular-campanulate, the tube being terete or slightly compressed in transverse section. The five corolla lobes are initially involute, becoming revolute during anthesis. The tube is normally white and translucent, the corolla lobes being yellow, but in *A. haemotomma* the latter are deep reddish-purple.

Cypselas

The term 'cypsela' is used in preference to achene to describe the fruit of the Compositae, as it is derived from a bicarpellate syncarpous inferior ovary, fused with the pericarp, testa and hypanthium (after Fahn, 1967).

The cypselas are heteromorphic ; those of ray florets are morphologically quite distinct from those of the disc florets. The ray cypselas are trigonous (e.g. sect. *Argyranthemum* and sect. *Sphenismelia*, Fig. 3a, e), terete or semiterete (e.g. sect. *Preauxia*, Fig. 3s, t). They can be erect (e.g. *A. broussonetii*, Fig. 3j) or arcuate, with a convex dorsal surface and a concave ventral surface (e.g. sect. *Argyranthemum*, Fig. 3a–d). There are usually 1 to 4 wings, varying in shape from a large coriaceous expansion (Fig. 3a–d) to a thin hyaline cristate extension of the margin (Fig. 3j, k, p). Sects. *Monoptera* and *Preauxia* are typically wingless (Fig. 3s, t, w).

Disc cypselas are obconical-turbinate or clavate, and are strongly laterally compressed, irregularly 4-angled or terete in transverse section. They are 1-winged (e.g. sect. *Argyranthemum*, Fig. 3f, h), 2-winged (e.g. *A. broussonetii*, Fig. 3l, m) or wingless (e.g. *A. pinnatifidum*, *A. adauctum*, Fig. 3q, r, x, y). Wings vary in shape from a cuneiform coriaceous ventral keel (e.g. sect. *Argyranthemum*) to a cristate margin (e.g. sect. *Monoptera*, Fig. 3h, q).

In transverse or longitudinal section the individual compositional components of the fruit wall are impossible to identify anatomically. However, the cypsela wall can conveniently be divided into three distinct layers : the epicarp consisting of a single row of rectangular parenchymatous cells slightly thickened with sclerenchyma in the corners ; the mesocarp composed of numerous layers of irregularly

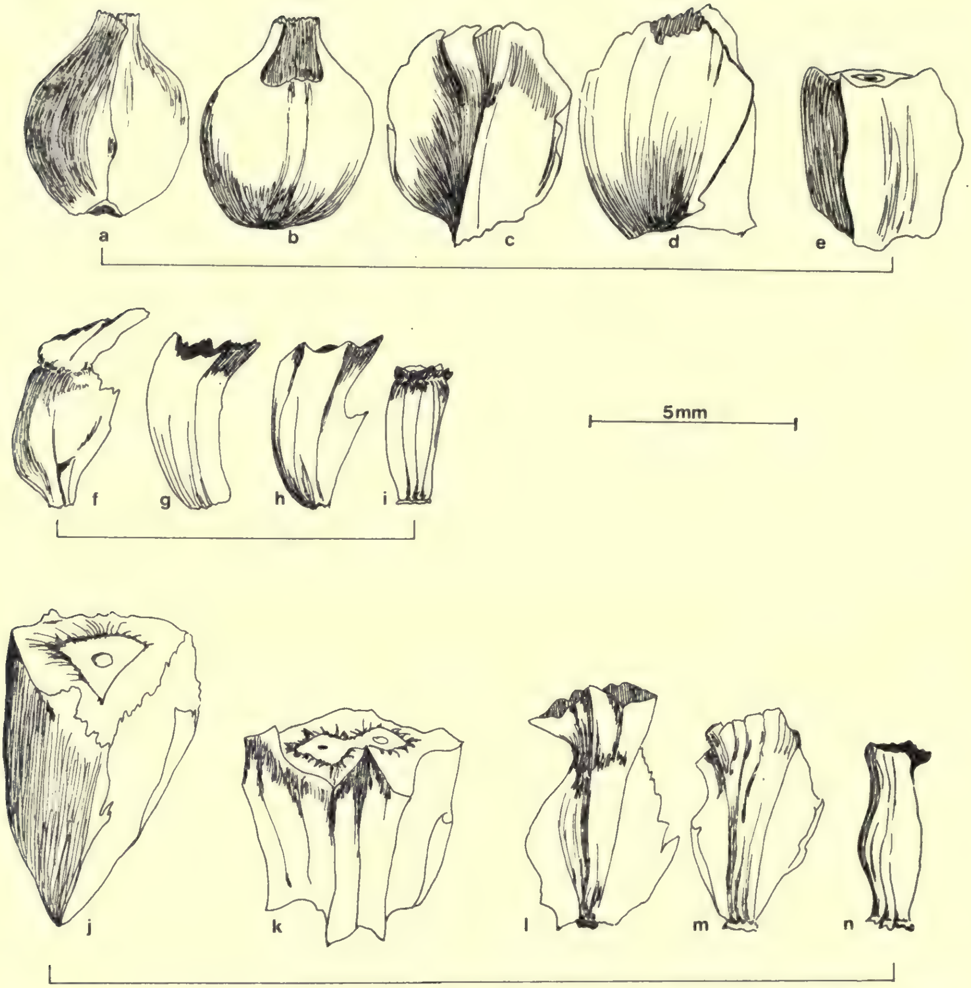

Fig. 3. Cypselas of *Argyranthemum* species grouped by taxonomic section: Section *Argyranthemum*: a, ventral surface, b, dorsal surface of ray cypsela of *A. gracile*; c, ventral surface, d, dorsal surface of ray cypsela of *A. winteri*; e, ventral surface of cypsela of *A. callichrysum*; f, lateral surface of disc cypsela of *A. dissectum*; g, h, i, lateral surface of disc cypselas of *A. frutescens* subsp. *frutescens*; Section *Sphenismelia*: j, ventral surface of ray cypsela of *A. broussonetii*; k, ventral surface of ray cypsela of *A. webbii*; l, lateral surface of disc cypsela of *A. broussonetii*; m, n, lateral surface of disc cypselas of *A. hierrense*.

shaped, tightly fitting, longitudinally arranged cells, variously thickened with sclerenchyma, vascular bundles, consisting entirely of lignified vessels and fibres, being found in this central layer; the endocarp consisting of a double row of regularly arranged rectangular cells lining the pericarp cavity between the mesocarp and the embryo. The cotyledons appear as two semi-terete lobes orientated in either anterior-posterior or transverse positions relative to the floral axis.

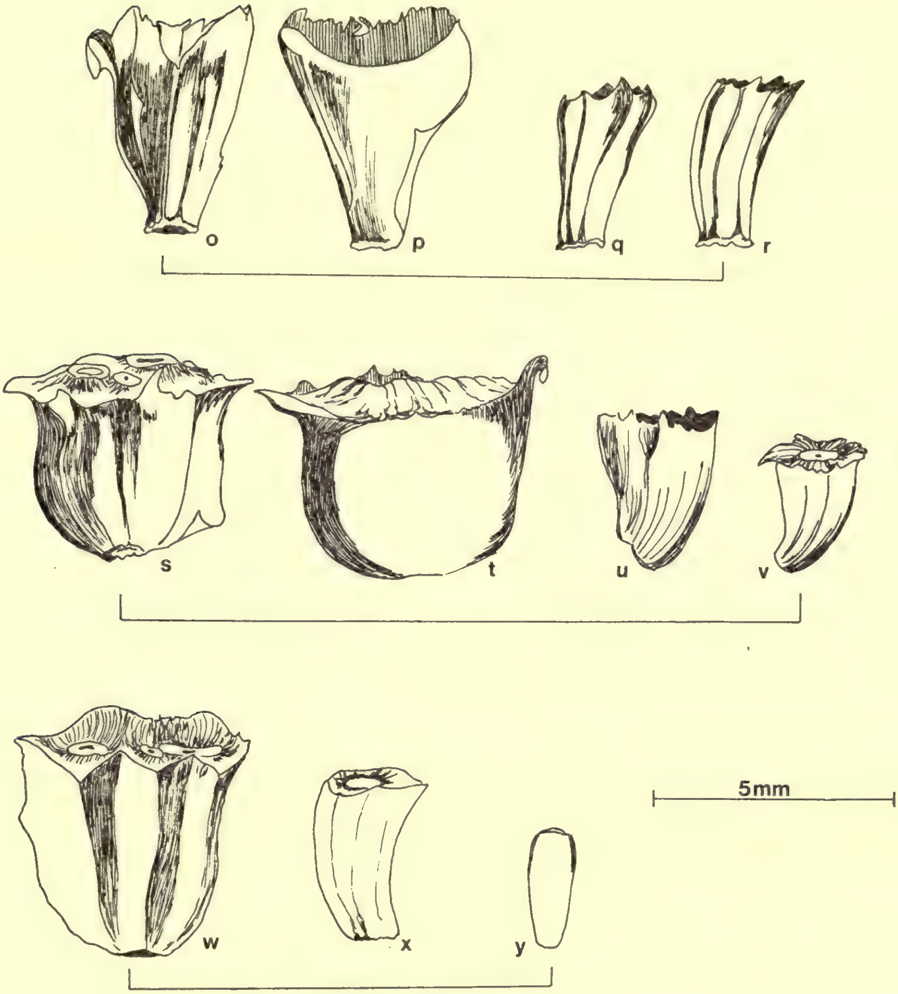

FIG. 3 (cont'd). Cypselas of *Argyranthemum* species grouped by taxonomic section: Section *Stigmatotheca*: o, ventral surface, p, dorsal surface of ray cypsela of *A. pinnatifidum*; q, ventral surface, r, lateral surface of disc cypsela of *A. pinnatifidum*; Section *Monoptera*: s, ventral surface, t, dorsal surface of ray cypsela of *A. filifolium*; u, v, lateral surface of disc cypselas of *A. filifolium*; Section *Preauxia*: w, ventral surface of ray cypsela of *A. adauctum*; x, y, lateral surface of disc cypselas of *A. adauctum*.

The epicarp of the cypsela is smooth and devoid of superficial structures, although the pericarp is irregularly folded or ridged in some species. The epicarp and mesocarp of adjacent ray cypselas are frequently coalesced (e.g. *A. hierrense*, *A. webbii*, *A. callichrysum* and *A. adauctum*, Fig. 3k, s, t, w), with occasional instances of fusion in both ray and disc cypselas (e.g. sect. *Monoptera*). Several specimens of *A. filifolium* have been observed with all of the cypselas in a capitulum completely coalesced to form a single dispersal unit.

In all species the cypselas have truncate bases encircled by a small ridge, which is presumably associated with abscission from the receptacle. At the distal end of the cypsela there is a small circular, semi-circular or triangular mark with a conspicuous central ring left by the abscission of the corolla and style (Fig. 3j, s, v, w). The colour ranges from white or yellow to chestnut brown, red-brown or black, the apex frequently being tinged with purple (e.g. sect. *Monoptera*).

Photographs of cypselas from several Canary Islands species are given in Borgen (1972).

Pappus

The variation in pappus morphology is generally greater than for other cypsela characters in *Argyranthemum*, particularly in sects. *Stigmatotheca*, *Argyranthemum* and *Sphenismelia*. The pappus consists of a scarious or coriaceous corona (Fig. 3a–d, f–h, l, m), a corneal or coriaceous ridge (Fig. 3e, w), or one or two corniculate spines (Fig. 3s, t). Margins are entire or sinuate-dentate. In sects. *Sphenismelia* and *Stigmatotheca*, the pappus often differs on ray and disc cypselas. In some species (e.g. *A. tenerifae*) the pappus may also vary in disc cypselas of the same capitulum. *A. adauctum* in sect. *Preauxia* sometimes has a rudimentary marginal ridge, but usually lacks a pappus completely (Fig. 3x, y).

In species with a coroniform pappus (e.g. *A. frutescens*, *A. gracile*, *A. foeniculaceum*, etc.) the pappus of the ray cypselas, and occasionally of the outer series of disc florets, is dimidiate and secund. The pappus projects centripetally from the ventral edge of the cypsela and is absent along the dorsal edge. This development is mainly influenced by the sloping position of the cypsela on the convex-conical receptacle and deflexion of the ray florets during anthesis.

CHROMOSOME NUMBERS

All species of *Argyranthemum* hitherto investigated from natural populations are diploid, with a basic number of $x = n = 9$ and a somatic chromosome number of $2n = 18$ (Tahara, 1915 ; Harling, 1951 ; Larsen, 1958, 1960 ; Borgen, 1969, 1970 ; Bramwell *et al.*, 1971). During the course of the work new counts have been made for six species, two subspecies of *A. frutescens* and two subspecies of *A. adauctum*, and previous counts have been confirmed at least once in all other taxa. In all of these cases the plants were found to be diploid, with 18 somatic chromosomes. The detailed results of these cytological studies are being reported elsewhere (Humphries, 1975).

Triploids ($2n = 27$) have only previously been reported in garden populations of *A. frutescens* (Tahara, 1915 ; Shimotomai, 1937 ; Harling, 1951 ; Dowrick, 1952). Similarly in this study, all meiotic preparations from pollen mother cells of buds fixed in the field have shown the diploid condition. However, in root tip mitoses and pollen mother cell preparations made from cultivated specimens of the only natural hybrid, *A. coronopifolium* × *frutescens* subsp. *frutescens*, plants with somatic numbers varying from $2n = 18$ to $2n = 36$ have been detected. It seems possible that genetic disturbances have occurred during meiosis giving rise to unbalanced gametes in the hybrid plants and in turn resulting in the formation of aneuploids, triploids and tetraploids which are normally suppressed in natural conditions.

Since the Chrysanthemineae form a fairly clear-cut natural group, it is of interest to consider briefly the chromosome numbers of other genera related to *Argyranthemum.* Although the basic number of the subtribe is $x = 9$, a wide range of chromosome counts from $2n = 18$ to $2n = 198$ have been reported (Dowrick, 1952). Variation in chromosome numbers (of authentic material) are due almost entirely to the formation of polyploids which are largely distributed in two regional centres of Central and Southern Europe and Eastern China and Japan. A great deal of evidence has been assembled to show that polyploids of Europe, belonging mainly to the genus *Leucanthemum*, are neo-endemic allopolyploids predominantly occupying alpine regions in areas left by retreating glaciers after the Pleistocene period (Villard, 1970). Similarly, it has been suggested that the majority of the oriental polyploid species, which belong mainly to the genus *Dendranthema* Desmoul. (*Chrysanthemum* L. sensu lato), have been produced by successive waves of hybridization and allopolyploidy, but also in a few cases by autopolyploidy, as a response to local ecological conditions (Shimotomai *et al.*, 1956 ; Tanaka, 1959a, b, c ; Kaneko, 1961). In Macaronesia all taxa of the Chrysantheminae are diploid, apart from a single tetraploid population of *Tanacetum ptarmicaeflorum* Schultz Bip. (Larsen, 1960).

TAXONOMIC RELATIONSHIPS WITHIN *ARGYRANTHEMUM*

As pointed out above (p. 169) and originally indicated by Schultz Bipontinus (1844a) the cypselas are perhaps the most characteristic infra-generic morphological features in *Argyranthemum.* On the basis of variation in cypsela shape and size, wing form and pappus morphology, coupled with various vegetative characters, it is possible to recognize five distinct sections within the genus.

The geographical distribution of each section is influenced by a pronounced ecological preference closely correlated with the altitudinal distribution of vegetation zones in the Canary Islands and to a lesser known extent of water availability on Madeira and the Salvage Islands (Table 2). Individual details of climax components, habitat conditions and limits of vegetation zones in relation to the position, altitude and climate of the Macaronesian Islands, and the Canary Islands in particular, can be found in the works of Webb and Berthelot (1835–1850), Ceballos & Ortuño (1951), Cifferi (1962), Oberdorfer (1965), Bramwell (1971) and Sunding (1972).

Ecological adaptive radiation to different habitats within each of the vegetation zones of the Canary Islands accounts for about 80% of the species diversity in *Argyranthemum.* Species density and section distribution have a more or less direct correlation with habitat diversity and availability in the different vegetation zones on each of the islands (Table 2 ; Fig. 4). On Tenerife, with the greatest land surface area ($\simeq$ 1880 km^2), the maximum number (5) of different vegetation zones in the Canary Islands (Table 2), and a wide range of climatic conditions, one finds nine species from three sections representing some 40% of the total infrageneric variation in Macaronesia. Lanzarote, on the other hand, with its single lowland xerophytic zone, invariable, desert-like climatic conditions and a relatively small surface area, contains only one isolated species, *A. maderense* (Fig. 4).

TABLE 2

The principal vegetation zones of the Canary Islands

Vegetation zone	Altitude (m)	Distribution	Characteristics of the vegetation zones
Alpine violetum	2700–3500	Tenerife	Dominated by a single species; *Viola cheiranthifolia*
Sub-alpine leguminous scrub	1900–2700	Tenerife and La Palma	Dominant species include *Spartocytisus supranubius*, *Nepeta teydea*, *Echium wildpretii*, and *Argyranthemum frutescens*
Pine Savannah	200–2000	Hierro, La Palma Tenerife and Gran Canaria	Dominated by *Pinus canariensis*, but often broken down into sub-climax communities as a result of forestry activities. Predominant scrub species include *Chamaecytisus proliferus*. On the southern slopes of Tenerife, *Juniperus phoenicea* scrub is also present
Laurel forest	600–1500	La Gomera, La Palma and Tenerife	Dominant species include *Apollonias barbujano*, *Persea indica*, *Ocotea foetans* and *Laurus azorica*. Great destruction of the laurel forest in recent times has led to the development of secondary vegetation. The most widespread sub-climax communities include *Erica arborea*, *Myrica faya* and *Ilex canariensis* (Fayal-brezal)
Lowland xerophytic zone	0–600 (–800)	All islands	Many vegetation types and different communities. Dominant families include stem and leaf succulents of the *Euphorbiaceae* and the *Crassulaceae*. Other important families include the *Compositae*, *Caryophyllaceae* and the *Liliaceae*.

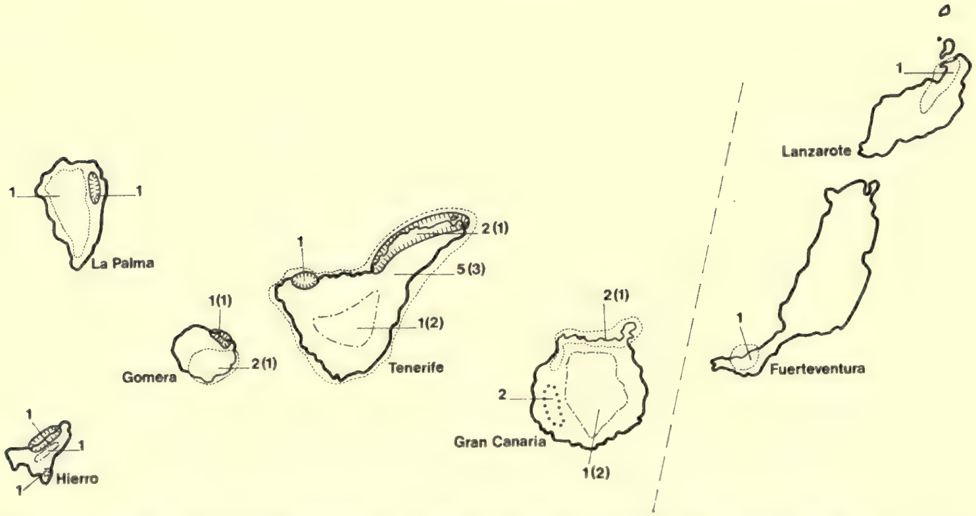

FIG. 4. Distribution of Sections of *Argyranthemum* in the Canary Islands. . . . . . , Section *Argyranthemum*; ⊥⊥⊥⊥, Section *Sphenismelia*; . . . . . , Section *Monoptera*; -·-·-·, Section *Preauxia*. The figures are the numbers of species in each area, with the number of subspecies in parentheses.

Section *Argyranthemum*

Section *Argyranthemum* consisting of 13 widely different species is by far the largest and most complex group in the genus, occupying predominantly xerophytic habitats, but also montane and sub-alpine habitats in all of the Canary Islands (Fig. 4), the Salvage Islands and Madeira. Its greatest development is found in the western Canary Islands and especially on Tenerife, where five species (*A. frutescens, A. lemsii, A. gracile, A. foeniculaceum* and *A. tenerifae*) all occur. Two of these species (*A. frutescens* and *A. gracile*) dominate the lowland xerophytic zone around the island periphery (Figs 5, 6, 12) and, though basically similar morphologically, can readily be distinguished from one another and are allopatrically and ecologically isolated. *A. frutescens* is the most widespread species in the section and is divided into a number of subspecies occurring in a variety of localities on Tenerife, Gran Canaria, Gomera and La Palma. It is perhaps best considered as an actively evolving taxon at an early stage of fragmentation. As well as the seven subspecies there are a number of closely related vicariant taxa to *A. frutescens* including *A. thalassophilum* from the Salvage Islands, *A. dissectum* from Madeira and *A. sventenii* from Hierro.

A second species group (*A. winteri, A. lidii, A. haouarytheum* and *A. callichrysum*) represent the cliff-montane and forest vicariants of the Canary Islands within section *Argyranthemum*. The species are very similar morphologically but are separable on differences of leaf dissection, of flower colour, and of inflorescence structure. Two of the species, *A. winteri* and *A. lidii*, are very narrowly restricted endemics confined to single localities on the western mountains of Feurteventura and Gran Canaria respectively (Figs 14, 16). *A. callichrysum* is a little more widespread, being a dominant form of the xerophytic localities in the Gomeran mountains (Fig. 18). The last species of this group, *A. haouarytheum*, is the most distinctive and variable of montane taxa, widespread in western pine forest habitats on the island of La Palma (Fig. 11). It occupies a special ecological position in section *Argyranthemum* in so much as all other *Pinus canariensis* forests in the Canary Islands are dominated by the polymorphic *A. adauctum* of the monotypic section *Preauxia*.

The three remaining species in the section, *A. foeniculaceum, A. tenerifae* and *A. maderense*, are all morphologically very distinctive and do not have any immediately recognizable relatives within the genus. All three species are ecologically distinct and the habit and leaf morphology are closely correlated with habitat. *A. foeniculaceum* is an obligate chasmophyte on Tenerife, occurring as two disjunct population groups of inland sheltered cliffs on Miocene basalt substrata (Fig. 9). Between the two populations one finds more recent coverings of Pliocene basalts and volcanic lavas of the Quaternary epoch. The disjunction between the two populations is best explained by the prevention of reinvasion of the intermediate habitats by *A. foeniculaceum* because of the drastically changed ecology, and competition from more adaptable plants.

The sub-alpine species *A. tenerifae* grows on cinders and volcanic debris at about 2000 m in the geologically most recent area on Tenerife (Fig. 12), the Cañadas Caldera, where volcanic eruptions have been reported as late as the 20th century.

The morphological relationships of this distinctive nanophanerophyte with other species is rather obscure, suggesting that either it represents an adaptation to the extreme conditions of this barren region or it is an immigrant now extinct in its original source localities. An interesting phylogenetic point which stems from morphological observations on *A. tenerifae* is that morphological divergence is not necessarily indicative of species age. What is more likely in areas of rapidly changing environmental conditions such as those of the Cañadas region is that evolutionary rates are quite different from those in the old stable cliff (or forest) habitats, which might have remained unchanged for millions of years.

The geographically most isolated species of the Canaries group, *A. maderense*, occurs as a rare coastal chasmophyte on the rocks of Famara on Lanzarote (Fig. 13). The pale yellow ligules and the succulent, ± sessile, pinnatilobed leaves with wide internodes reflect also the taxonomically isolated position of this species.

Section *Sphenismelia*

The five broad-leaved species of this section (*A. coronopifolium, A. broussonetii, A. hierrense, A. webbii* and *A. haemotomma*) have an obligate ecological preference for the moist laurel forests and halophyte communities of the north-facing slopes and coastal areas of the western Canary Islands and Madeira. The two morphologically similar taxa *A. broussonetii* and *A. webbii* represent a vicariant species pair dominating the forest-covered northern slopes of Tenerife, Gomera and La Palma.

A. hierrense is a distinct third member of the section, also occurring in the laurel forests and the lower reaches of the pine forests on Hierro, but it is primarily a coastal chasmophyte of very low altitudes.

A. coronopifolium is perhaps the rarest of all species in the genus *Argyranthemum*, existing only as a single population of a few plants on the steep cliffs of Teno in N.W. Tenerife. It is in danger of becoming extinct in the near future in its pure form, as interspecific hybrids with *A. frutescens* are invading the stand and backcrossing with the parental plants (Humphries, 1973).

The exact affinities of *A. haemotomma* with other members of the section are somewhat obscure. The species is endemic to the small desert islands of Deserta Grande and Bugio, off Madeira. It is similar in habit to the Tenerife chasmophyte, *A. coronopifolium*, but differs in the smaller bipinnatifid leaves and distinctive deep red colour of the corollas. Plants with a similar flower colour in the Chrysanthemum complex are found only in the annual species, *Chrysanthemum carinatum* Schousb., from continental North Africa and the Salvage Islands (see p. 156).

Section *Stigmatotheca*

This section contains one polymorphic species, *A. pinnatifidum* from Madeira. It is distinguished from its nearest relatives of section *Sphenismelia* by the vestigial wings, lack of pappus and irregular ribbing of both ray and disc cypselas. The candelabra branching pattern and crowding of leaves around the base of the peduncles is shared by *A. foeniculaceum* in section *Argyranthemum*, but the unique development of large, ovate ± entire leaves represents an extreme development of the foliage repertoire in *Argyranthemum*. The distribution of this species is unusual in that it occurs at all altitudes on the island of Madeira. A partial explanation for this phenomenon is that Madeira is much cooler and wetter than the Canary Islands and does not develop such distinctive vegetation zonation.

Section *Monoptera*

This section contains two species (*A. filifolium* and *A. escarrei*) both of which are very narrow endemics from the island of Gran Canaria. They are both adapted to extremely xerophytic habitats, having a reduced habit, thin pinnatisect leaves and diminutive floral parts. The distinctive clavate cypselas with a corniculate pappus are quite unlike any other species in the genus although their nearest relative on the basis of cypsela morphology is *A. adauctum* in section *Preauxia.*

The distribution and morphology of the two species never overlap and both taxa exist as a small number of populations. It is difficult to distinguish the subtle ecological differences of their individual habitats but *A. escarrei* tends to favour a slightly wetter climate and higher altitude than *A. filifolium* and probably represents a divergent upland ecotype.

Section *Preauxia*

This monotypic section containing *A. adauctum* is found primarily in the endemic montane *Pinus canariensis* forest and savannah of Gran Canaria, Tenerife and Hierro. *A. adauctum* subsp. *gracile,* however, occurs in more open situations and extends to the intensely arid lowland xerophytic scrub of southern Gran Canaria and subsp. *erythrocarpon* is found in the tree heath—broad-leaved evergreen forests of Hierro. The fruit morphology is unique amongst Macaronesian species in that the disc cypselas are quite wingless and not compressed. The species is extremely variable and a number of different subspecies can be recognized. As with *A. frutescens,* the component subspecies are groups of closely related ecologically adapted local populations, insufficiently diverged to be considered as separate species.

ARGYRANTHEMUM Webb ex Schultz Bip.

ARGYRANTHEMUM Webb ex Schultz Bip. in Webb & Berthel., Phyt. Canar. 2 : 245, 258 (1844).

Chrysanthemum L., Sp. Pl. 2 : 887 (1753) ; Gen. Pl., ed. 5 : 379 (1754), pro parte.
Pyrethrum Zinn, Cat. Pl. Gott. : 414 (1757), pro parte.
Argyranthemum Webb & Berthel., tom. cit. : t. 92 (Mar. 1839), *nom. nud.*
Chrysanthemum sect. *Argyranthemum* (Webb ex Schultz Bip.) Bentham in Bentham & Hooker, Gen. Pl. 2 (1) : 424 (1873).
Chrysanthemum subgen. *Argyranthemum* (Webb ex Schultz Bip.) Harling in Acta Hort. Berg. 16 : 50 (1951).

Suffruticose *perennials* 40–150 cm ; stems procumbent to ascending, sulcate. *Leaves* ± entire or variously dissected. *Inflorescence* lax, corymbose ; capitula pedunculate, (1–) 2–50 per branch ; peduncles erect, striate. *Involucre* hemispherical ; bracts imbricate, in 3–4 series, the veins thick, herbaceous, green, the margins scarious. *Receptacle* convex-conical ; scales absent. *Ray florets* 6–38 mm, female, ligulate, yellow, white or pink ; *disc florets* 2–4 mm, hermaphrodite, tubular-campanulate, pentamerous, yellow or deep purple-red, usually with sparse glandular hairs on corolla-tube. *Anthers* 5, laterally connate with short tails and triangular apex. *Styles* bifid, the base swollen, the apices truncate-pencilliate. *Cypselas* heteromorphic, smooth or irregularly ribbed, without pericarpic secretory cells. *Ray cypselas* trigonous, with 1–3 wings, or wingless, turbinate, usually arcuate, sometimes coalesced into groups of 2–9 ; pappus completely or partially coroniform, or absent. *Disc cypselas* abconical, terete, 4-angled or laterally compressed, with 1–2 wings or wingless, sometimes coalesced with the ray cypselas ; pappus completely or partially coroniform, or absent. *Cotyledons* transversely orientated ; *embryo-sac* bisporic. $2n = 18$.

Type species : *A. frutescens* (L.) Schultz Bip., based on *Chrysanthemum frutescens* L.

Endemic to Macaronesia : Madeira, the Salvage Islands and the Canary Islands ; introduced in the Azores.

The question of whether the generic name *Argyranthemum* was validly published by Webb & Berthelot in March 1839 is debatable. It first appeared on Tab. 92 of the *Phytographia Canariensis*, which was part of livraison 37 of the work (Stearn, 1937). This plate gives illustrations of two plants : '*Argyranthemum frutescens* Nob. *γ grandiflorum*, *δ cuneiforme*'. Of the first, only a habit drawing is given, but the illustration of the second has both this and analyses of the flower. The analytical figures are numbered, but there is no key to the numbering on the plate. The problem is : can this plate be regarded as an illustration with analysis of a monotypic new genus based on a new species and as thus giving the generic name valid publication?

On the one hand, there is nothing to connect the name *Argyranthemum frutescens*, or either of the varietal epithets, with previously published species. Nevertheless the characters of the plant illustrated make it obvious that it is closely related to *Chrysanthemum*, and the names *C. frutescens* L., *C. grandiflorum* (Willd.) DC., and *C. grandiflorum* [var.] *δ cuneiforme* DC. all applied to plants from the Canaries.

The argument for rejecting the view that the plate gives valid publication to the generic name, on the other hand, is that, since the only illustration with analysis on it is of a non-typical variety, the pictures do not necessarily show the essential features of the species and genus. This view seems the more cogent, especially as the fact that Webb & Berthelot did not regard the species as new became apparent when the text of their work was issued, and it is adopted here.

When the name next appeared, on Tab. 94 of the *Phytographia Canariensis* in May 1839, it was on an illustration of '*Argyranthemum anethifolium* Nob.' As this adds a second species to the genus, it cannot give the name valid publication. Accordingly *Argyranthemum* is treated here as having been first validly published in 1844, in the text of the *Phytographia Canariensis.* This means that all the names on Plates 90–96 of the work are not validly published. This has the advantage that all those that were intended as new combinations can be treated as such, and do not have to be regarded as names of new species with Webb's specimens as their types.

KEY TO SPECIES

- Ray cypselas wingless ; pappus a coriaceous rim or absent :
  - Stem and leaves hispid to tomentose . . . 22. *adauctum*
  - Stem and leaves glabrous :
    - Ray cypselas not coalesced into groups :
      - Disc cypselas with one or two wings . . . 15. *broussonetii*
      - Disc cypselas wingless . . . 19. *pinnatifidum*
    - Ray cypselas coalesced into groups of 2–8 :
      - Leaves sessile . . . 22. *adauctum*
      - Leaves petiolate :
        - Leaves oblong, pinnatisect, subulate-filiform, scarcely divided ; stems slender ; ray florets 6–12 mm . . . 20. *filifolium*
        - Leaves obovate, pinnatisect to bipinnatisect ; stems robust ; ray florets 10–40 mm :
          - Primary leaf-lobes obtriangular in outline, attenuate at the base . 21. *escarrei*
          - Primary leaf-lobes ovate to obovate in outline, not attenuate at the base :
            - Ray-florets 20–38 mm ; disc cypselas usually 2-winged . 15. *broussonetii*
            - Ray-florets 12–22 mm ; disc cypselas usually 1-winged . . 17. *webbii*
- Ray cypselas (1 –) 2–4-winged ; pappus usually coroniform :
  - Leaves ± entire to pinnatilobed or bipinnatilobed :
    - Ligules pale yellow . . . 7. *maderense*
    - Ligules white :
      - Disc cypselas without wings ; involucre 6–15 mm in diameter . 19. *pinnatifidum*
      - Disc cypselas 1- to 2-winged ; involucre 12–22 mm in diameter . 14. *coronopifolium*
  - Leaves bipinnatifid to bipinnatisect :
    - Leaf-lobes 0·3–3·0 (–3·5) mm wide ; filiform to linear-lanceolate :
      - Leaves 2–3 (–4)-fid ; stems slender . . . 5. *gracile*
      - Leaves 4–60-fid ; stems robust :
        - Leaves glaucous, crowded around the base of the peduncles, the lower caducous 4. *foeniculaceum*
        - Leaves green, on all parts of the stem, the lower persistent :
          - Primary leaf-lobes 2–6 . . . 1. *frutescens*
          - Primary leaf-lobes 6–14 (–20) :
            - Involucre 11–15 mm in diameter . . . 3. *haouarytheum*
            - Involucre 6–10 (–11) mm in diameter . . . 13. *sventenii*
    - Leaf-lobes 2·0–8·0 mm wide ; ovate to obovate :
      - Disc florets purple-red ; ligules usually pink to white ; disc cypselas 2-winged 18. *haemotomma*
      - Disc florets yellow ; ligules white or yellow ; disc cypselas 1-winged or without wings :
        - Ray cypselas coalesced in groups of 2–5 :
          - Primary leaf-lobes 2–5 . . . 16. *hierrense*
          - Primary leaf-lobes 6–14 . . . 12. *callichrysum*
        - Ray cypselas not coalesced :
          - Inner involucral bracts triangular-lanceolate . . . 6. *tenerifae*
          - Inner involucral bracts obovate-spathulate with obtuse expanded apices :
            - Leaves with 2–6 (–8) primary lobes :
              - Outer involucral bracts with an extended fleshy keel along the midrib 11. *thalassophilum*
              - Outer involucral bracts rounded (but not keeled) along the midrib :
                - Peduncles villous towards the apex ; leaf-lobes cuspidate . . 2. *lemsii*
                - Peduncles glabrous ; leaf-lobes acute to obtuse. . . 1. *frutescens*
            - Leaves with 6–18 primary lobes :
              - Involucre 12–20 mm in diameter :
                - Leaves bipinnatifid . . . 8. *winteri*
                - Leaves bipinnatisect-pectinate . . . 10. *dissectum*

Involucre 6–12 mm in diameter :
  Leaf-lobes acute ; ray florets yellow or white . . . 12. *callichrysum*
  Leaf-lobes obtuse, uncinate ; ray florets white . . . . 9. *lidii*

Section 1. ***ARGYRANTHEMUM***

ARGYRANTHEMUM sect. ARGYRANTHEMUM, sect. typ. gen. (Text-fig. 4).

Chrysanthemum sect. *Magarsa* DC., Prodr. 6 : 65 (1838).
Stigmatotheca sect. *Otopappus* Schultz Bip. in Webb & Berthel., Phyt. Canar. 2 : 255 (1844).

Plants glabrous or hispidulous on the leaf midribs only. *Leaves* pinnatilobed to pinnatisect or bipinnatisect, petiolate. *Ray florets* white, yellow or pink. *Ray cypselas* trigonous, arcuate, 2-winged with 2 large coriaceous lateral wings and a small keel-like ventral wing ; pappus coroniform or absent. *Disc cypselas* obconical, laterally compressed, 1-winged ; pappus coroniform or absent.

1. ***Argyranthemum frutescens*** (L.) Schultz Bip. in Webb & Berthel., Phyt. Canar. 2 : 264 (1844). (Text-fig. 5–6.)

Chrysanthemum frutescens L., Sp. Pl. 2 : 887 (1753). – DC., Prodr. 6 : 65 (1838). – Masferer in An. Soc. esp. Hist. nat. 10 : 207 (1881) reimpr. ut Rec. Bot. Tenerife : 131 (1881). – Burchard in Biblthca bot. 98 : 199 (1929). – Ceballos & Ortuño, Veg. Fl. For. Canar. Occid. : 439 (1951).
Pyrethrum frutescens (L.) Gaertn., Fruct. Sem. Pl. 2 : 431 (1791). – Choisy in Buch, Phys. Beschreib. Canar. Ins. : 149 (1825).
Matricaria frutescens (L.) Desrouss. in Lam., Encycl. Méth., Bot. 3 : 730 (1792).
Chrysanthemum floridum Salisb., Prodr. Stirp. Hort. Chapel Allerton : 202 (1796), *nom. superfl.*
Chrysanthemum foliosum Brouss., Elench. Pl. Hort. Bot. Monsp. : 16 (1805), *nom. nud.*
Chrysanthemum grandiflorum Brouss., tom. cit. : 15 (1805), *nom. nud.*
Chrysanthemum speciosum Brouss. in Pers., Syn. Pl. 2 : 463 (1807), *nom. synon.*
Pyrethrum grandiflorum Willd., Enum. Pl. Hort. Berol. : 904 (1809). – Choisy in Buch, loc. cit.
Chrysanthemum grandiflorum (Willd.) DC, Cat. Pl. Hort. Bot. Monsp. : 96 (Mar. 1813)[1] ; Prodr. 6 : 66 (1838), excl. [var.] α *adauctum* et [var.] δ *cuneiforme*.
Pyrethrum speciosum Willd., Enum. Pl. Hort. Berol., Suppl. : 60 (1814).
Chrysanthemum fruticosum Buch in Abh. preuss. Akad. Wiss. 1816–17 : 375 (1819), *nom. nud.* (? sphalm. pro *C. frutescens*).
Pyrethrum crithmifolium sensu Link in Buch, Phys. Beschreib. Canar. Ins. : 149, 165 (1825), non Willd.
Chrysanthemum intermedium Hort. Monsp. ex DC., Prodr. 6 : 66 (1838), *nom. synon.*
Argyranthemum frutescens Webb in Webb & Berthel., Phyt. Canar. 2 : t. 91 (1840), *nom. invalid.*

Stems 20–80 cm, procumbent to erect, branches throughout or only at the base, glabrous to hispidulous. *Leaves* 1·5–8 × 0·5–6 cm, obovate to linear-lanceolate in outline, pinnatisect to bipinnatisect (rarely tripinnatisect), petiolate, glabrous to hispidulous, coriaceous, succulent ; primary lobes 2–10, opposite to alternate, 2–40 × 0·5–6 mm, lanceolate to linear-lanceolate ; secondary lobes 2–6, opposite to alternate, 1–10 × 0·5–4 mm, linear-lanceolate to dentate, obtuse or acuminate. Leaf clusters common in the axils of cauline leaves. *Inflorescence* corymbose, with 4–30 capitula ; peduncles up to 16 cm ; bracts leaf-like or simply linear-lanceolate in outline. *Involucre* 6–22 mm in diameter ; bracts in 3 series, triangular to obspathulate or linear-lanceolate ; inner bracts scarious, with an expanded hyaline apex. *Ray florets* 7–15 × 2–5 mm, white, 1–3-fid at the apex ; *disc florets* 2–4 mm, corolla lobes yellow. *Ray cypselas* 3–5 × 2–4·5 mm, trigonous, arcuate, 3-winged ; 2 lateral wings, expanded, coriaceous, with convex dorsal surface ; ventral wing obtriangular ; pappus coroniform, dimidiate, the margin laciniate ; *disc cypselas* 2·5–4 × 1–2 mm, obconical, laterally compressed to sometimes ± terete, arcuate in outer series, 1-winged, irregularly ribbed ; pappus coroniform, dimidiate, with laciniate margins to sometimes vestigial or absent. *Flowering period* : throughout the year.

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[1] *Chrysanthemum grandiflorum* Lapeyr., Hist. Abr. Pl. Pyrénées: 527 (May 1813), *nom. superfl.* was published about two months later than this name.

Tenerife, Gran Canaria and Gomera. Also reported from a single locality on Hierro.

Widespread in maritime and lowland areas from 5–700 m ; common on coastal cliffs, rocky shores and sand dunes ; grows on a variety of basal rocks, from Miocene basalts to recent lava flows.

The holotype of this species is in Hort. Cliff. (BM), Linnaeus having adopted unchanged in the *Species Plantarum* the phrase name he used for the species in the *Hortus Cliffortianus;* the specimen is labelled : 'Leucanthemii canariense sapore pyrethri H. C. Chrysanthemum frutescens'.

This species displays in the most extreme form the taxonomic problem of assessing allopatric differentiation of the kind encountered in *Argyranthemum.* At first sight a number of distinct morphological entities can be recognized, but attempts at their precise definition reveal that they overlap and intergrade to a considerable degree.

Most of the problem lies in the fact that the characters that most obviously distinguish the subspecies in the field (plant height and branching position) are difficult, if not impossible, to see in most herbarium specimens. Instead of relying on such characters, a conscious attempt has been made to select several quantitative morphological characters, including leaf-lobe width, number of leaf-lobes and capitulum diameter, to indicate the pattern of allopatric diversity which occurs below the species level and to give some criteria for herbarium identification. There are no immediate sharp discontinuities between populations but there is a continuum of variation, broken into nodal peaks in the distribution curves for each character corresponding with geographical distribution. It can be argued that such differences call for taxonomic lumping, a situation which readily proceeds to the recognition of a single taxonomic entity. Such a solution is unacceptable however, owing to the wide range of recognizable discontinuous variants the taxon would embrace relative to other less widespread species. Figures 5 and 6 provide data for variation of four such characters in samples of *A. frutescens,* selected from all parts of its distribution range.

In the absence of sharp breaks, the boundary between the infra-specific groups must necessarily be defined somewhat arbitrarily. The chosen rank of subspecies (Figs 5, 6A, B, C, etc.) at which to recognize these groupings is obviously open to

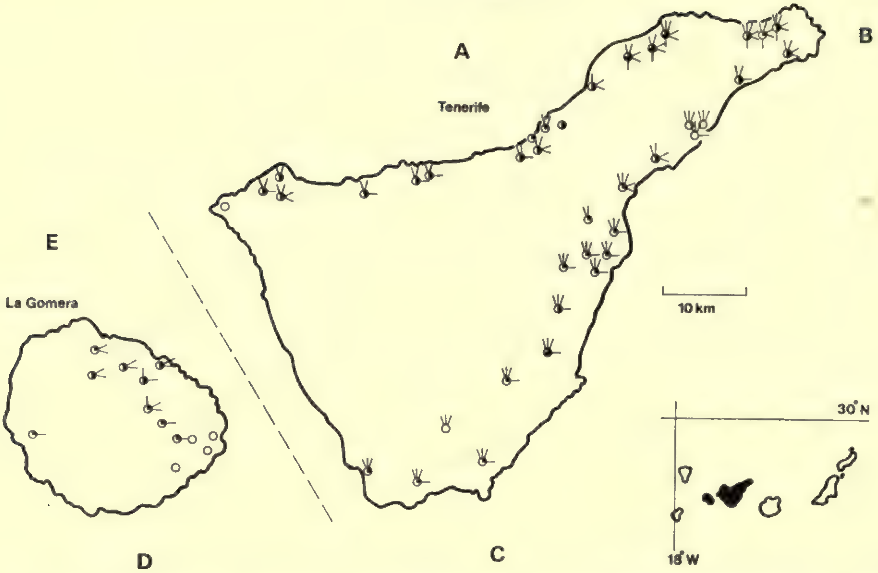
A
B
Tenerife
E
La Gomera
10 km
30°N
18°W
D
C

FIG. 5. Distribution and variation of subspecies of *Argyranthemum frutescens* on Tenerife and Gomera: A, subsp. *frutescens*; B, subsp. *succulentum*; C, subsp. *gracilescens*; D, subsp. *parviflorum*; E, subsp. *foeniculaceum*.

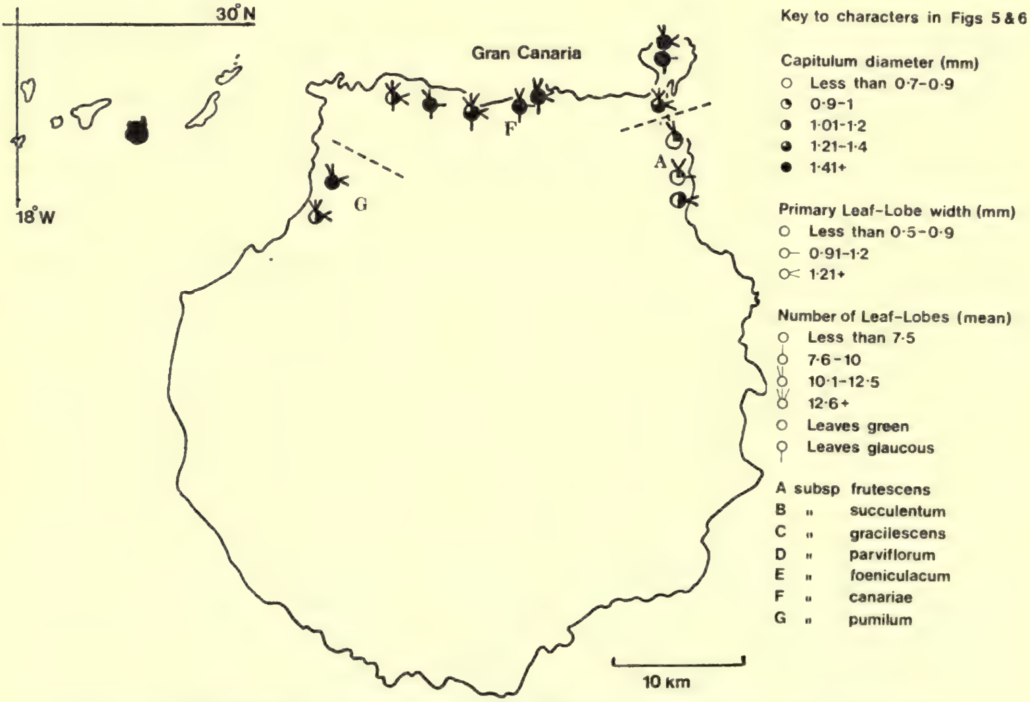
30°N
18°W
Gran Canaria
F
A
G
10 km
Key to characters in Figs 5 & 6
Capitulum diameter (mm)
○ Less than 0·7–0·9
◔ 0·9–1
◑ 1·01–1·2
◕ 1·21–1·4
● 1·41+
Primary Leaf-Lobe width (mm)
○ Less than 0·5–0·9
○– 0·91–1·2
○< 1·21+
Number of Leaf-Lobes (mean)
○ Less than 7·5
7·6 – 10
10·1–12·5
12·6+
○ Leaves green
Leaves glaucous
A subsp frutescens
B " succulentum
C " gracilescens
D " parviflorum
E " foeniculacum
F " canariae
G " pumilum

FIG. 6. Distribution of subspecies of *Argyranthemum frutescens* on Gran Canaria: A, subsp. *frutescens*; F, subsp. *canariae*; G, subsp. *pumilum*.

question, but populations are grouped into subspecies when there is a distinct morpho-geographical facies which can be distinguished by at least one character from other populations within the species. The concept normally applies to vicariant populations adapted to local ecological conditions, and in this way it is used in a sense similar to that of Du Rietz (1930) and present-day taxonomists (Hedberg, 1958 ; Heywood, 1958a ; Valentine & Löve, 1958).

KEY TO SUBSPECIES

Ligules 4–7 mm :
Leaf rachis 1–2 mm wide ; leaves glaucous . . . . . . e. *foeniculaceum*
Leaf rachis usually less than 1 mm wide ; leaves green . . . . d. *parviflorum*
Ligules 7–15 mm :
Involucre 10–16 mm in diameter :
Leaf-lobes 3–8 (–10) :
Leaves 4–8 cm, glaucous, glabrous ; primary lobes 2–4 cm . e. *foeniculaceum*
Leaves 1–4 cm, green, glabrous to scabridulous ; primary lobes 0·3–2·5 cm a. *frutescens*
Leaf-lobes 7–20 :
Leaf-lobes filiform, 0·5–1·2 mm wide . . . . c. *gracilescens*
Leaf-lobes broad, succulent, 1·2–5·0 mm wide :
Leaf-lobes acute. . . . . g. *pumilum*
Leaf-lobes obtuse to cuspidate . . . . f. *canariae*
Involucre 6–10 mm in diameter :
Leaf-lobes 3–11 :
Leaves 4–8 cm, glaucous, glabrous ; primary lobes 2–4 cm . . e. *foeniculaceum*
Leaves 1–4 (–6) cm, green, glabrous to scabridulous ; primary lobes 0·3–2·5 cm a. *frutescens*
Leaf-lobes 7–20 :
Leaf-lobes linear-lanceolate, 0·5–2·0 mm wide . . . . . . c. *gracilescens*
Leaf-lobes ovate-lanceolate, 2·0–5·0 mm wide :
Leaf-lobes acute . . . . g. *pumilum*
Leaf-lobes obtuse . . . . b. *succulentum*

a. subsp. ***frutescens.*** (Text-fig. 2A 1, 3g, h, i.)

Pyrethrum frutescens α Choisy in Buch, Phys. Beschreib. Canar. Ins. : 149 (1825).
Argyranthemum frutescens [var.] γ *grandiflorum* Webb in Webb & Berthel., Phyt. Canar. 2 : t. 92, fig. dextr. (1839), *nom. nud.*
Argyranthemum frutescens [var.] α *linnaeanum* Webb in Webb & Berthel., tom. cit. : t. 91, fig. 1, 3–20 (1840), *nom. invalid.*
Argyranthemum frutescens forma *major* Schultz Bip. in Webb & Berthel., tom. cit. : 264 (1844).

Stems 30–70 cm erect, branched throughout, glabrous to hispidulous. *Leaves* 1·5–5 × 0·5–3 cm, glabrous to hispidulous ; primary lobes 2–6 (–8), subopposite to alternate 5–18 × 0·5–2 mm ; secondary lobes dentate, acute. *Involucre* 6–12 mm in diameter. *Ray florets* 12–15 × 2·5–3 mm.

Tenerife : Bco de Masca, 0–200 m, 13 Sept. 1966, *Lems 6282* (MICH). Casas de Teno Bajo, 5 Apr. 1971, *Bramwell & Humphries 3275* (BM ; RNG). El Fraile, 5 Apr. 1971, *Bramwell & Humphries 3282* (BM ; RNG). Buenavista, Mar. 1888, *Ball* (Z). Same locality, 19 June 1956, *Lems 2640* (L ; MICH). Same locality, 6 Sept. 1965, *Kaae* (C). Icod, 2 Jan. 1921, *Børgesen 307* (C). Same locality, 6 June 1890, *Murray* (RHS). San Juan de la Rambla, in *Cistus* scrub, Dec. 1968, *Bramwell 483* (RNG). Same locality, 3 Aug. 1954, *Lems 2093* (MICH). Bco. Cabezas near Orotava, 5 m, 25 Oct. 1968, *Bramwell 274* (RNG). Martinez, Orotava, 50 m, May 1922, *Burchard 84* (G ; Z). Same locality, 9 May 1884, *Ball* (Z). Puerto de la Cruz, 20 m, 8 May 1957, *Larsen* (C). Same locality, 10 Mar. 1855, *Perraudière* (P). Same locality, 15 Apr. 1855, *Perraudière* (P ; S). Same locality, *Webb* in herb. Schultz Bip. (P). Punta Brava, 13 Oct. 1969, *Kaae* (C). La Cuesta, 300 m, Sept. 1906, *Pitard* (G ; L ; P). Monte de Zafira, 3 June 1894, *Murray* (G ; K). Igueste de San Andrés, 200 m, 18 June 1971, *Bramwell & Humphries 3461* (BM ; RNG). San Andrés, 1954, *Wall 554* (S). Bco. de Bufadero, 21 Jan. 1905, *Pitard & Proust 198* (G ; L ; P ; S). Santa Cruz, Bco. de la Cruz, *c.* 180 m, 16 Mar. 1937, *Asplund 341* (G ; K). Same locality, 100 m, 27 May 1901, *Bornmüller 2472* (G ; P ; W ; Z). Same locality, 2 Mar. 1855, *Perraudière* (P ; W). Same locality, *Webb* in herb. Schultz Bip. (P). Playa de la Viuda, between Guimar and Candelaria, 18 Apr. 1971, *Bramwell & Humphries 3460* (BM ; RNG). *Broussonet* (C ; Z). *Broussonet* in herb. Willdenow (B). 1816, *Christian Smith* (G-DC). Ex herb. Daniel de la Roche (G-DC). *Webb* in herb. Schultz Bip. (K ; P).

Gran Canaria : Catalina Park, Las Palmas, 16 Jan. 1965, *Kaae* (C). Agaete, 27 Dec. 1960, *Hummel* (S).

Cult., Hort. Cliff. (BM, holotypus).

North coast of Tenerife from Baranco de Masca and the cliffs of El Fraile to Puerto de la Cruz, and the south coast from Igueste on the Punta de Anaga to the Punta de Guimar. East coast of Gran Canaria from Las Palmas to La Estrella, and on the west coast around Agaete (Figs 5, 6).

Typically found on wet coastal cliffs and barrancos, but grows as a weed in disturbed areas and waste ground in towns ; 5–300 m. Several populations are also known from the xerophytic *Euphorbia canariense* and *E. balsamifera* scrub communities on the south slopes of the Anaga peninsula.

A reduction in size and leaf succulence is found along the south coast of Tenerife between Candelaria and Guimar, forming a gradual transition to *A. frutescens* subsp. *gracilescens*. Natural hybrids between *A. frutescens* subsp. *frutescens* and *A. coronopifolium* have been detected at Teno, on the west peninsula of Tenerife. Putative hybrids between this subspecies and *A. broussonetii* (*Chrysanthemum tanacetifolium* Desf., Cat. Pl. Hort. Reg. Paris ed. 3 : 447 (1829), *nom. nud.*) are also reported from the Barranco de Bufadero, near San Andrés on the south coast of the Anaga peninsula of Tenerife.

b. subsp. **succulentum** C. J. Humphries, subsp. nov. (Text-fig. 2A 2.)

Pyrethrum crithmifolium sensu Link in Buch, Phys. Beschreib. Canar. Ins. : 149, 165 (1825) non Willd., quoad specim. ex Tenerife.

Chrysanthemum coronopifolium Masferer in An. Soc. esp. Hist. nat. 10 : 208 (1881) reimpr. ut Rec. Bot. Tenerife : 132 (1881), pro parte, non *Pyrethrum coronopifolium* Willd. nec specim. a Teno.

Chrysanthemum crithmifolium Christ in Bot. Jb. 9 : 146 (1887), non *Chrysanthemum crithmifolium* (Willd.) Buch (1819).
Argyranthemum frutescens var. *crithmifolium* Pitard & Proust, Îles Canar., Fl. Archipel. : 230 (1908) pro parte, non *Pyrethrum crithmifolium* Willd. nec specim. a Gran Canaria.
Chrysanthemum frutescens var. *crithmifolium* Ceballos & Ortuño, Veg. Fl. For. Canar. Occid. : 439 (1951) pro parte, non *Pyrethrum crithmifolium* Willd.

Caules 30–50 cm procumbentes, omnino ramosi, glabri. *Folia* 2–7 × 2–4 cm, succulenta, glabra, glauca ; lobi primarii 2–6, 6–25 × 1–5 mm, oppositi vel suboppositi ; lobi secundarii 2–4, 2–10 × 1–4 mm, alterni, obtusi. *Involucrum* 6–8 (–10) mm diametro. *Radiorum flosculi* 10–14 × 2·5–4 mm.

Stems 30–50 cm, procumbent, branched throughout, glabrous. *Leaves* 2–7 × 2–4 cm, succulent, glabrous, glaucous ; primary lobes 2–6, 6–25 × 1–5 mm, opposite to subopposite ; secondary lobes 2–4, 2–10 × 1–4 mm, alternate, obtuse. *Involucre* 6–8 (–10) mm in diameter. *Ray florets* 10–14 × 2·5–4 mm.

Tenerife: Taraconte, in regione maritima, 31 Jan. 1905, *Pitard & Proust 197* (G ; L ; P, holotypus). La Paz, Puerto de la Cruz, 1889, *Christ* (Z). Santa Ursula, Barranco de la Cruz, 150 m, 16 Mar. 1933, *Asplund 341* (G ; S). Bajamar, 21 Feb. 1969, *Asplund* (S). Bajamar, Punta Hidalgo, 7 Apr. 1967, *Kaae* (C). Playa del Roque, Taganana, 20 m, 9 Apr. 1971, *Bramwell & Humphries 3376* (BM ; RNG). Taganana, 5 June 1900, *Bornmüller 814* (G ; P ; W ; Z). Same locality, *Pitard* (P). Sierra Anaga, Roques de la Animas, 18 Apr. 1969, *Bramwell 1348* (RNG). East of Taganana, 50 m, 3 Apr. 1967, *Bally 12943* (G). *Simony 20 & 21* (W).

North coast of Tenerife from La Paz, north-east of Puerto de la Cruz, to Punta de Santiago, east of Taganana. Invariably found on wet coastal cliffs, commonly associated with halophyte communities ; 50–100 m. The cushion habit and succulent stems and leaves most resemble populations of subsp. *canariae*. The plants can easily be distinguished, however, by their smaller flowers and grey glaucous appearance.

Willdenow described *Pyrethrum crithmifolium* from specimens collected on Tenerife by Broussonet. I have examined photographs of these specimens and *P. crithmifolium* is clearly conspecific with *P. foeniculaceum* Willd. (= *A. foeniculaceum*). Specimens of succulent-leaved varieties of *A. frutescens* collected by L. von Buch. from the north coasts of Tenerife and of Gran Canaria were cited by Link (*loc. cit.*) under the name *Pyrethrum crithmifolium* Willd. The Gran Canarian populations were later considered by Christ (in Bot. Jb. 9 : 145 (1887)) to be a variety of *A. frutescens* (viz. *A. frutescens* var. *canariae*). Pitard later considered the plants from the north coast of Tenerife to be a distinct variety of *A. frutescens*, but followed Link's misapplication of the epithet *crithmifolium*, making a new combination based on *Pyrethrum crithmifolium* Willd. Since no validly published name has been applied to this subspecies it is described as new above.

c. subsp. **gracilescens** (Christ) C. J. Humphries, comb. et stat. nov. (Text-fig. 2A 3.)

Chrysanthemum frutescens [var.] β *hispidum* DC., Prodr. 6 : 66 (1838).
Chrysanthemum frutescens var. *gracilescens* Christ in Bot. Jb. 9 : 145 (1887).

Argyranthemum gracile sensu Pitard & Proust, Îles Canar., Fl. Archipel. : 230 (1908) ; non Webb ex Schultz Bip.

Chrysanthemum gracile sensu Burchard in Biblthca bot. 98 : 199 (1929) pro parte, excl. specim. a Arona, Adege et Guia, non Masferer. – Ceballos & Ortuño, Veg. Fl. For. Canar. Occid. : 439 (1951) pro parte, quoad specim. a ora meridionali-occidentali Tenerifae.

Stems 20–50 (–70) cm, branched towards the base, glabrous to hispidulous. *Leaves* 1·5–7 × 1–3·5 cm, hispidulous on the midrib ; primary lobes 4–10, subopposite, 6–25 × 0·5–2 mm ; secondary lobes 2–8, subopposite to alternate, 2–10 × 0·1–1 mm, acute. *Involucre* 9–12 mm in diameter. *Ray florets* 10–14 × 2–3·5 mm.

Tenerife: Between Sobradillo and Barranco Grande, 2 Apr. 1971, *Bramwell and Humphries 3178* (BM ; RNG). Between Barranco Hondo and Candelaria, 2 Apr. 1971, *Bramwell & Humphries 3179* (BM ; RNG). Guimar, 1882, *Hillebrand* in herb. Christ (Z, holotypus). Guimar, Monte de Los Guimes, 20 Mar. 1933, *Asplund 450* (G). Ladera de Guimar, 400 m, 2 Mar. 1969, *Bramwell 846* (RNG). Same locality, 2 Apr. 1971, *Bramwell & Humphries 3198* (BM ; RNG). Same locality, 550–650 m, 6 Jan. 1966, *Lems 6541* (MICH). Same locality, 20 Feb. 1855, *Perraudière* (P). Same locality, 24 Feb. 1855, *Perraudière* (P). Arajo, 580 m, 20 Oct. 1965, *Lems 6122* (MICH). Bco. de Escobonal, 400 m, 3 Apr. 1971, *Bramwell & Humphries 3203* (RNG). Playa de San Marcos, 50 m, 8 Aug. 1965, *Lems 5575* (MICH). Valle de Arico, Avesce, 1882, *Hillebrand* in herb. Christ (Z). Valley Seco, 10 Mar. 1884, in herb. Christ (Z). Bco. de Tamadaya, 600 m, 3 Apr. 1971, *Bramwell & Humphries 3208* (BM ; RNG). 1 km north of Medano, 100 m, 4 Apr. 1971, *Bramwell & Humphries 3256* (BM ; RNG). Same locality, 17 Oct. 1965, *Kaae* (C). Same locality, 16 Mar. 1967, *Kaae* (C). Between Granadilla and San Miguel, 20 Oct. 1965, *Kaae* (C). Guaza near Los Christianos, 21 Mar. 1967, *Kaae* (C). *Bolle 230* (P). Feb. 1845, *Bourgeau 16* (FI ; P ; TCD ; W ; Z). Dec. 1845, *Bourgeau 1237* (FI ; G ; P ; W). 1801, Broussonet (G-DC).

Widespread on the lower slopes and on the south coast of Tenerife from Sobradillo (near Santa Cruz) to Los Christianos on the southern peninsula of the island (Fig. 5).

Common in xerophytic communities of *Euphorbia canariensis*, *E. balsamifera*, *Launaea arborescens* and matorral on dry south-facing barrancos ; it grows in a variety of habitats such as cliffs, rocky slopes and sand dunes, and is frequently found as a weed in cultivated and urbanized areas ; 50–700 m.

d. subsp. ***parviflorum*** (Pitard & Proust) C. J. Humphries, stat. nov. (Text-fig. 2A 4.)

Argyranthemum frutescens var. *parviflorum* Pitard & Proust, Îles Canar., Fl. Archipel : 231 (1908).

Chrysanthemum frutescens var. *parviflorum* (Pitard & Proust) Ceballos & Ortuno, Veg. Fl. For. Canar. Occid. : 439 (1951).

Stems 30–60 cm, erect, branched from the base. *Leaves* 2–6 × 0·5–3 cm, glabrous; primary lobes 2–4, opposite to alternate, 2–25 × 0·5–2 mm ; secondary lobes 1–4 × 0·5–2 mm acute. *Involucre* 4–6 (–8) mm in diameter. *Ray florets* 4–7 × *c.* 1·5 mm.

La Gomera: Bco. de la Concepcion in aridis regionis maritimi, 8 Apr. 1905, *Pitard & Proust 196* (G ; L ; P, holotypus). Punta de San Cristobal, 5 m, 7 Apr. 1971, *Bramwell & Humphries 3363* (BM ; RNG). Same locality, 30 m, 27 May 1957, *Larsen* (C). San Sebastian, 14 Apr. 1901, *Bornmüller 2474* (G ; P ; W ; Z). Same locality, 27 May 1894, *Murray* (G). Same locality, 25 m, 1960, *Hummel* (S). Bco. de la Villa, 200 m, 3 Aug. 1969, *Bramwell 1943* (RNG). Same locality, 23 May 1894, *Murray* (W). Same locality, 200 m, 7 Apr. 1971, *Bramwell & Humphries 3360* (BM ; RNG). Same locality, 700 m, 3 July 1969, *Bramwell 1943 a* (RNG). Same locality, 7 km north of San Sebastian, 500 m, 6 Apr. 1971, *Bramwell & Humphries 3356* (BM ; RNG). La Carbonera, 22 July 1954, *Lems 2340* (L ; MICH). Valle Gran Rey, 400 m, 27 June 1969, *Bramwell 2271* (RNG).

Tenerife: Punta de Teno, 100 m, 4 May 1969, *Bramwell 1435* (RNG). Same locality, 50 m, 5 Apr. 1971, *Bramwell & Humphries 3274* (BM ; RNG). Buenavista, 27 Feb. 1845, *Bourgeau 823* (FI).

Widely distributed on Gomera along the south-eastern slopes and coastal areas around San Sebastian and along the mountains and north-west coast towards Hermigua. A single locality is also recorded for Valle Gran Rey, and on the Punta de Teno of Tenerife (Fig. 5).

Plants are usually found in xerophytic communities of *Euphorbia canariensis*, *E. regis-jubae* and *Kleinia neriifolia* between 5 and 500 m, but also in regenerative scrub communities of old *Laurus azorica* forest at higher altitudes near La Carbonera between 500 and 700 m.

This subspecies is similar to subsp. *gracilescens* in general appearance and foliage morphology. It differs by the diminutive floral parts, particularly in the size of the ray florets and cypselas. The habit is slightly more compact with branching from the base of the stem and with many peduncles in each inflorescence.

e. subsp. ***foeniculaceum*** (Pitard & Proust) C. J. Humphries, stat. nov. (Text-fig. 2A 5.)

Argyranthemum frutescens var. *foeniculaceum* Pitard & Proust, Îles Canar., Fl. Archipel. : 230 (1908).

Ismelia coronopifolia sensu Pitard & Proust, op. cit. : 232 (1908) quoad specim. a Gomera, non Schultz Bip.

Chrysanthemum coronopifolium sensu Ceballos & Ortuño, Veg. Fl. For. Canar. Occid. : 441 (1951) pro parte, quoad specim. a Gomera, non Masferer.

Stems 30–80 cm, branched throughout or only at the base, glabrous. *Leaves* 3–8 × 2–5 cm, glabrous, glaucous ; primary lobes 2–4, 8–40 × 1·5–2 mm, subopposite to opposite ; secondary lobes usually absent, rarely 1 or 2, 2–8 × *c.* 0·5 mm, acuminate. *Involucre* 6–12 mm in diameter. *Ray florets* 6–8 × 1·5–2·5 mm.

La Gomera: Agulo, in rupestribus, 300 m, 13 Apr. 1905, *Pitard 195* (G ; L ; Z, holotypus). Hermigua 200 m, 25 May 1957, *Larsen* (C). 3 km west of Agulo near Las Rosas, 500 m, 6 Apr. 1971, *Bramwell & Humphries 3352* (BM ; RNG). Agulo, 26 May 1894, *Murray* (K). Bco. de Vallehermoso near El Puerto, 25 m, 2 Jan. 1969, *Bramwell 463* (RNG). Same locality, 6 Apr. 1971, *Bramwell & Humphries 3348* (BM ; RNG). Same locality, 300 m, Apr. 1906, *Pitard* (G).

A subspecies of intermittent distribution along the north coast of La Gomera from Agulo to Vallehermoso (Fig. 5).

A locally common coastal subspecies in xerophytic communities of *Euphorbia canariensis* and *Kleinia neriifolia* between 25 and 200 m, and at higher altitudes in habitats dominated by *Adenocarpus foliolosus* scrub, between 200 and 500 m.

It is distinguished from all other subspecies by its deeply pinnatisect and sometimes trifid, glaucous leaves. The florets are similar to those in subsp. *parviflorum* but differ in having fewer peduncles and a taller, less compact habit, and by branching throughout the plant.

f. subsp. ***canariae*** (Christ) C. J. Humphries, stat. nov. (Text-fig. 2A 6.)

Pyrethrum crithmifolium sensu Link in Buch, Phys. Beschreib. Canar. Ins. : 149, 165 (1825) non Willd., quoad specim. a Gran Canaria.

Ismelia coronopifolia var. *angustifolia* Schultz Bip. in Webb & Berthel., Phyt. Canar. 2 : 272 (1844).

Chrysanthemum frutescens var. *canariae* Christ in Bot. Jb. 9 : 145 (1887).

Argyranthemum frutescens var. *canariae* (Christ) Pitard & Proust, Îles Canar., Fl. Archipel. : 230 (1908).

Argyranthemum frutescens var. *crithmifolium* Pitard & Proust, op. cit. : 230 (1908) pro parte, quoad specim. a Gran Canaria, non *Pyrethrum crithmifolium* Willd.

Ismelia coronopifolia sensu Pitard & Proust, op. cit. : 232 (1908), quoad specim. a Gran Canaria, non Schultz Bip.

Stems 20–50 cm, procumbent, branched throughout, glabrous. *Leaves* 3–8 × 2–4 cm, succulent, glabrous to sometimes glaucous; primary lobes 2–8, opposite to alternate, 6–18 × 2–5 mm ; secondary lobes 1–4, alternate, 2–10 × 2–3 mm, apiculate. *Involucre* 12–20 mm in diameter. *Ray florets* 15–30 × 3–5 mm.

Gran Canaria: En todas partes del norte de la Isla, 1882, *Hillebrand* in herb. Christ (Z, holotypus). La Isleta, Feb. 1905, *Pitard* (P). Confital, Feb. 1906, *Pitard* (P). Bañadero, 30 Apr. 1897, *Gelert* (C). Same locality, May 1892, *Murray* (G ; RHS ; W). San Felipé, 50 m, 17 Mar. 1971, *Bramwell & Humphries 3001* (BM ; RNG). Same locality, 200 m, 17 Mar. 1971, *Bramwell & Humphries 3002* (BM ; RNG). Moya, 60 m, *Bramwell 1226* (RNG). Same locality, 28 Oct. 1966, *Lems 6143* (MICH). La Cuesta de Silva, 100–200 m, Apr. 1924, *Burchard 238* (G ; S ; Z). Same locality, 2 May 1897, *Gelert* (C). Hermigua, 2 Feb. 1967, *Kunkel 10090* (G). Guia, Mar. 1896, *Collett* (K). Between Las Palmas and Telde, 29 Apr. 1890, *Murray* (K). Same locality, 30 Mar. 1901, *Bornmüller 2471* (G ; P ; W ; Z). Apr. 1846, *Bourgeau 489* (FI ; G ; K ; P ; TCD ; W ; Z). 1837, *Despreaux 196* (G).

Distributed in Gran Canaria from La Isleta on the north-east peninsula to Galdar on the north-west coast. Several collections have also been recorded on the east coast between Las Palmas and Telde (Fig. 6).

Occurs in halophyte communities along coastal rocks and cliffs and associated with *Astydamia latifolia* and *Euphorbia balsamifera* scrub communities at higher altitudes ; 25–200 m.

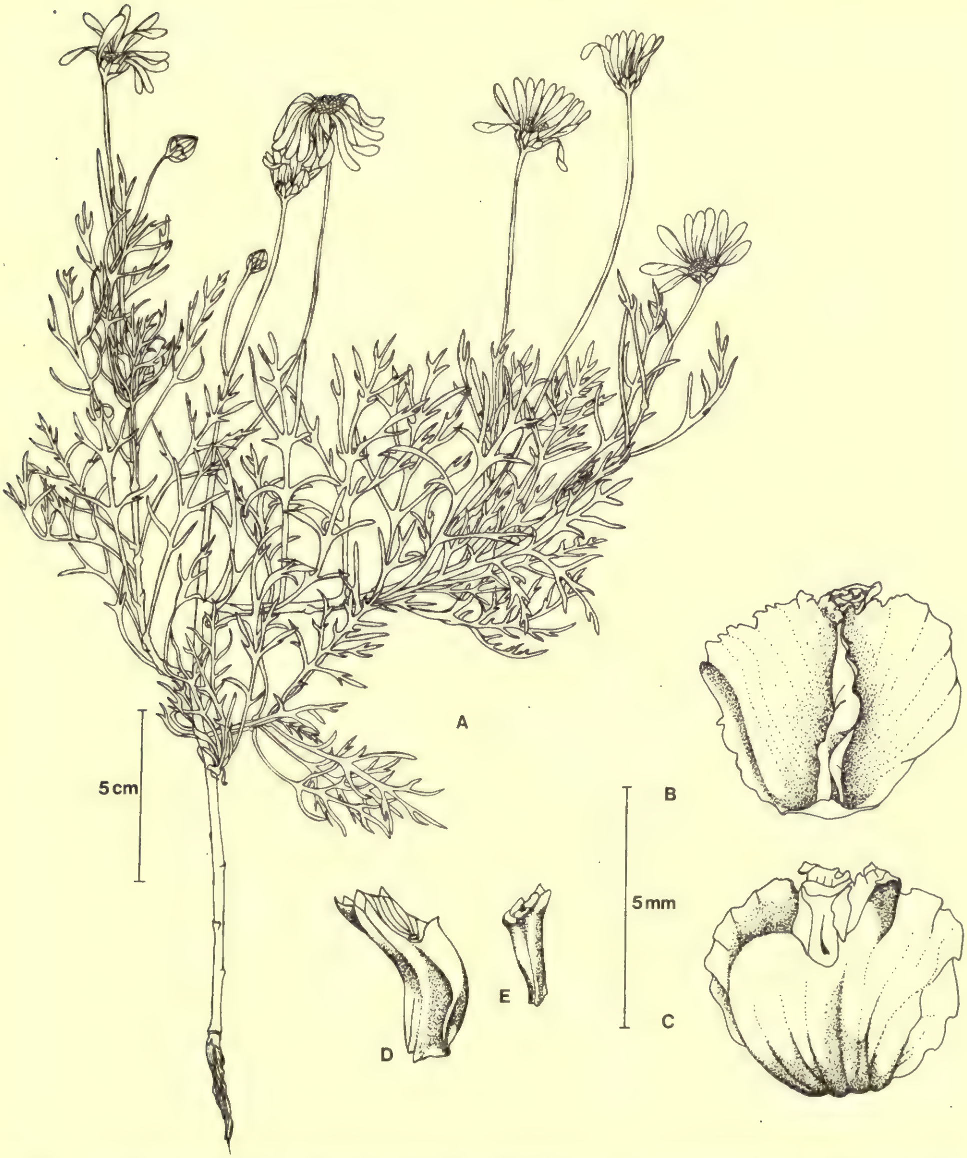

FIG. 7. *Argyranthemum frutescens* subsp. *pumilum* C. J. Humphries: A, whole plant; B, ventral view; C, dorsal view of ray cypsela; D, lateral view of disc cypsela of outer series; E, lateral view of disc cypsela of inner series.

g. subsp. **pumilum** C. J. Humphries, subsp. nov. (Text-fig. 2A 7, 7.)

Subsp. *foeniculaceo* affinis sed habitu magis compacto, floribus grandioribus, et foliis plus dissectis, imprimis differt.

Caules 30–50 cm, procumbentes, omnino ramosi, glabri. *Folia* 3·5–10·0 × 0·3–4·5 cm, bipinnatisecta, glabra; lobi primarii 2–8, oppositi vel alterni, 0·5–3·0 × 0·5–

3·5 cm; lobi secundarii 1–2, 2·0–10·0 × *c.* 0·2 mm, acuminati. *Involucrum* 12–14 mm diametro. *Radiorum flosculi* 12–22 × 2–4 mm (Fig. 7).

Stems 30–50 cm, procumbent, with branches in all parts, glabrous. *Leaves* 3·5–10·0 × 0·3–4·5 cm, bipinnatisect, glabrous; primary lobes 2–8, opposite to alternate, 0·5–3·0 × 0·5–3·5 cm; secondary lobes 1–2, 2·0–10·0 × *c.* 0·2 mm, acuminate. *Involucre* 12–14 mm in diameter. *Ray florets* 12–22 × 2–4 mm.

Gran Canaria: Bco. Laya del Risco, 750 m, 23 Mar. 1971, *Bramwell & Humphries 3155* (BM; RNG, holotypus). Same locality, 500 m, 23 Mar. 1971, *Bramwell & Humphries 3169* (BM; RNG).

A chasmophyte of dry coastal cliffs at Laya del Risco in xerophytic scrub, dominated by *Euphorbia balsamifera* and *Launaea arborescens*; 500–600 m.

2. ***Argyranthemum lemsii*** C. J. Humphries, sp. nov. (Text-fig. 2B, 8, 9.)

Ab *A. frutescens* subsp. *frutescens* foliorum lobis obspathulatis cuspidatis, pedunculis versus apicem villosis et bracteis externis involucri costis villosis differt.

Caules 50–60 cm, ascendentes, ramosi per tota planta, glabri. *Folia* 1–3·5 × 0·3–1·5 cm, ambitu obovata, pinnatifida vel bipinnatifida, petiolata, glabra vel hispidula, praecipue in costam; lobi primarii 2–6, 0·3–1·2 × *c.* 1·0 cm, subopposti, ambitu spathulati; lobi secundari subopposti, usque ad 3 mm longitudine, ad apicem cuspidati. *Inflorescentia* corymbosa, laxa, 2–10 capitulata; pedunculi 3–10 cm longi; bracteae foliiformae. *Involucrum* 8–11 mm diametro, bracteae series 3 continuas formantes, bracteae extimae parvae, triangularis, costis carnosis villosis, bracteae intimae obovatae vel oblongae, ad marginem et apicem expansae, hyalinae et scariosae. *Radiorum flosculi* 13–20 × 2·5–3·0 mm, albi, trifidi ad apicem; *discorum flosculi c.* 3 mm longi, lobis corollae flavis et tubis albidis. *Radiorum cypselae* 3–4 × 2–3·5 mm, trigonae, aliquantum obconicae, arcuatae, alis 3; pappus coroniformis, dimidiatus vel plus minusve absens ad marginem dorsalem; *discorum cypselae* 2–3 × 1–2 mm, turbinatae, a latere compressae vel plus minusve quadrangulares, ala 1 vel sine alam; pappus coroniformis dimidiatus ad marginem dorsalem seriei extinarum. *Florescentia* ignotus.

Stems 50–60 cm, ascending, branched throughout the plant, glabrous. *Leaves* 1–3·5 × 0·3–1·5 cm, obovate in outline, pinnatifid to bipinnatifid, petiolate, glabrous to hispidulous, particularly on the midrib; primary lobes 2–6, 0·3–1·2 × *c.* 1 cm, subopposite, obspathulate in outline; secondary lobes up to 3 mm, subopposite, cuspidate at the apex. *Inflorescence* corymbose, lax, with 2 to 10 capitula, villous at the apex; peduncles 3–10 cm long; bracts leaf-like. *Involucre* 8–11 mm in diameter, bracts forming 3 continuous series, outer bracts small, triangular in outline, the midrib fleshy, villous, the margin scarious; inner bracts obovate to oblong in outline, hyaline and scarious at the margins, expanded at the apex. *Ray florets* 13–20 × 2·5–3 mm, white, 3-fid at the apex; *disc florets c.* 3 mm, with corolla lobes yellow and the tube white. *Ray cypselas* 3–4 × 2–3·5 mm, trigonous, somewhat obconical, arcuate, 3-winged; pappus coroniform, reduced by half to ± absent on the dorsal edge; *disc cypselas* 2–3 × 1–2 mm, turbinate, laterally compressed to ± quadrangular, usually 1-winged, occasionally wingless; pappus coroniform, dimidiate on the dorsal edge of outer series. *Flowering period* unknown.

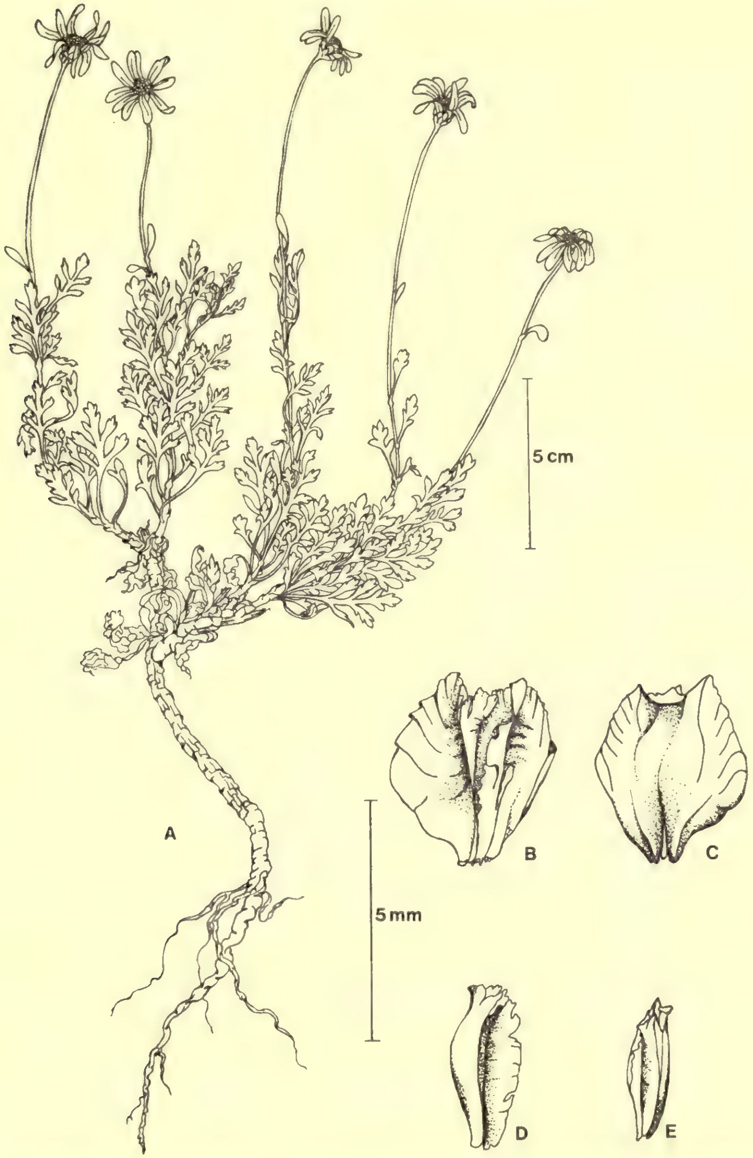

FIG. 8. *Argyranthemum lemsii* C. J. Humphries : A, whole plant ; B, ventral view, C, dorsal view of ray cypsela ; D, lateral view of disc cypsela of outer series ; E, lateral view of disc cypsela of inner series.

Holotypus: Tenerifae, semita propre Chamorga 600 m.s.m., leg. *K. Lems.* In herb. Univ. Michiganum servatus (MICH)! Isotypus in herb. Novi Eboraci servatus (NY)!

This species is named in honour of the late Kornelius Lems, a distinguished contributor to the biological knowledge of the Canary Islands.

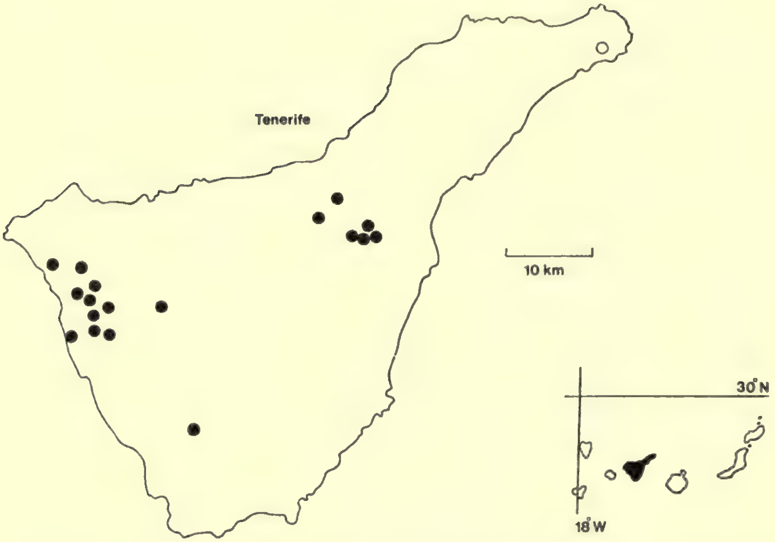

FIG. 9. Distribution of *Argyranthemum lemsii* (○) and *A. foeniculaceum* (●) on Tenerife.

A rare endemic of the Punta de Anaga from Tenerife (Fig. 9); known only from the single locality of Chamorga, and found in the Fayal-Brezal arboreal heath associated with *Myrica faya*, *Erica arborea* and *Ilex canariensis* between 500 and 700 m, on basal rocks consisting almost entirely of Miocene basalt.

The plants are low-growing shrubs with small hispidulous or glabrous leaves. They are readily distinguished from other species in the genus by the obspathulate cuspidate leaf-lobes (Fig. 2B) and the slight covering of villous hairs at the apex of the peduncles. There are no immediately discernible morphological affinities with any other taxa, except for a superficial resemblance of the habit to *A. frutescens* subsp. *frutescens*.

3. **Argyranthemum haouarytheum** Humphries & Bramwell, sp. nov. (Text-fig. 2C, 10, 11; Pl. 29b.)

Chrysanthemum coronopifolium var. *angustum* Christ in Bot. Jb. 9 : 146 (1887) '*angusta*'.

Argyranthemum webbii sensu Pitard & Proust, Îles Canar., Fl. Archipel : 231 (1908), non Schultz Bip.

Chrysanthemum webbii sensu Burchard in Biblthca bot. 98 : 200 (1929), non Masferer. – Ceballos & Ortuño, Veg. Fl. For. Canar. Occid. : 440 (1951).

A. callichryso Svent. similis, sed foliis minoribus cum lobis lineari-lanceolatis angustis, floribus majoribus et praeserti pappo coroniformi dentato irregulari, differt.

Caules 60–100 m, ascendentes, ramosi per tota planta, glabri. *Folia* 5–16 × 2–5 cm, obovata, bipinnatisecta, petiolata, glabra; lobi primarii 4–12, 2–6 × 0·1–0·4 cm, suboppositi, lanceolati; lobi secundarii 0·5–2 × *c.* 0·1 cm, alterni vel suboppositi, acuti. *Inflorescentia* corymbosa, laxa, 2–30 capitulata; pedunculi

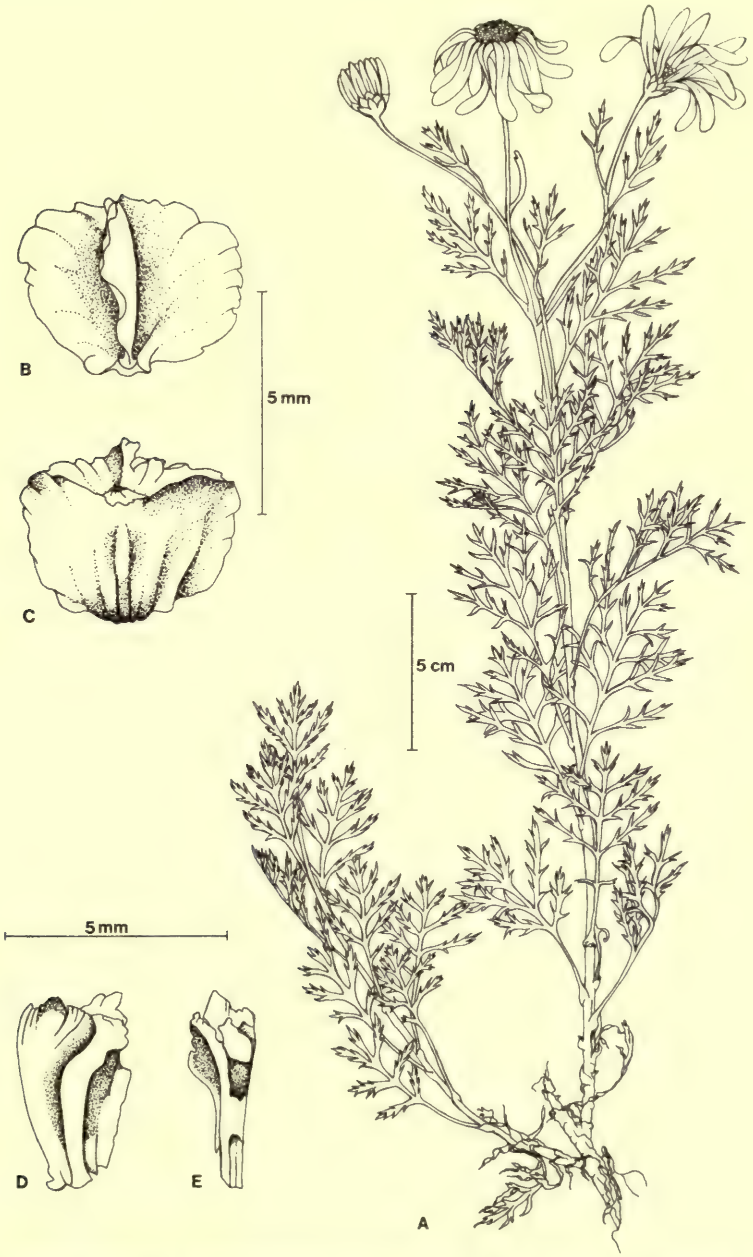

FIG. 10. *Argyranthemum haouarytheum* Humphries & Bramwell: A, whole plant; B, ventral view, C, dorsal view of ray cypsela; D, lateral view of disc cypsela of outer series; E, lateral view of disc cypsela of inner series.

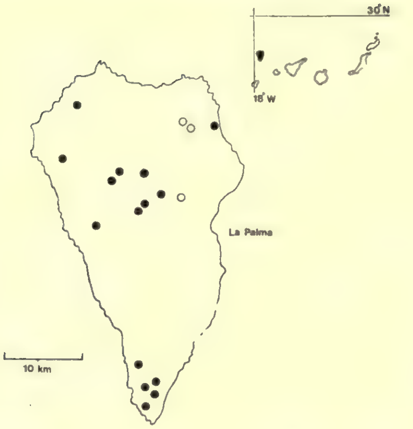

FIG. 11. Distribution of *Argyranthemum haouarytheum* (●) and *A. webbii* (○) on La Palma.

12–15 cm ; bracteae lineo-lanceolate. *Involucrum* 11–15 mm diametro ; bracteae series 3 formantes ; bracteae extimae triangulares, scariosae, carnosae ad costam, bracteae intimae rectangulares vel obovatae, et ad apicem expansae, scariosae et hyalinae. *Radiorum flosculi* 15–21 × 2–5·2 mm, albi, trifidi ad apicem ; *discorum flosculi* c. 3 mm longi, lobis corollae flavis et tubis albis. *Radiorum cypselae* 3–5 × 2·6–4·5 mm, turbinatae, trigonae, trialatae, duae alae laterales expansae et coriaceae, ala ventralis parva, obtriangularis ; pappus coroniformis, irregulariter dentatus ; *discorum cypselae* 2–4·5 × 1·7–3 mm, obconicae, a latere compressae, unialatae ; pappus coroniformis irregulariter dentatus. *Florescentia* Mars ad Octavium.

Stems 60–100 cm, branched throughout, glabrous. *Leaves* 5–16 × 2–5 cm, obovate, bipinnatisect, petiolate, glabrous ; primary lobes 4–12, 2–6 × 0·1–0·4 cm, subopposite, lanceolate ; secondary lobes 0·5–2·0 × *c.* 0·1 cm, alternate to subopposite, acute. *Inflorescence* corymbose, lax with 2–30 capitula ; peduncles 12–15 cm ; bracts linear lanceolate. *Involucre* 11–15 mm in diameter ; bracts in 3 series ; outer bracts triangular, scarious, fleshy towards the midrib ; inner bracts rectangular to obovate, scarious and hyaline towards the expanded apex. *Ray florets* 15–21 × 2–5·2 mm, white, 3-fid at the apex ; *disc florets c.* 3 mm, with yellow corolla lobes and whitish tubes. *Ray cypselas* 3–5 × 2·6–4·5 mm, turbinate, trigonous, with 3 wings ; the 2 lateral wings expanded and coriaceous, the ventral wing, small, obtriangular ; pappus coroniform, irregularly dentate ; *disc cypselas* 2–4·5 × 1·7–3 mm, obconical, laterally compressed, 1-winged. *Flowering period:* March to October.

La Palma: Bco. de Candelaria, Tigarafe, 700 m, in pineto subumbroso, 12 June 1969, *Bramwell 1919* (RNG, holotypus ; LTR ; SEV). Santa Cruz, Caldereta, 6 June 1923, *Sprague & Hutchinson 1296* (K). Puerto de los Sauces, 30 Oct. 1845, *Bourgeau 1* (P). Roque de Teneguia, 150 m, 15 Apr. 1971, *Bramwell & Humphries 3417* (BM ; RNG). Same locality, 15 Apr. 1971, *Bramwell & Humphries 3410*

(BM; RNG). Fuencaliente, 150 m, 8 July 1969, *Bramwell 1853* (RNG). Same locality, 9 June 1969, *Bramwell 1876* (LTR; RNG). Volcan de San Antonio, 400–600 m, 28 May 1966, *Lems 7697* (MICH). Heliño, between Fuencaliente and Los Llanos, 15 Apr. 1971, *Bramwell & Humphries 3414* (RNG). Bco. de las Angustias, 800 m, 18 Apr. 1901, *Bornmüller 2475* (G; K; L; P; W; Z). Same locality, *Hillebrand* in herb. Christ (Z). Same locality, 16 Apr. 1971, *Bramwell & Humphries 3442* (RNG). Same locality, Caldera de Taburiente, 1 Aug. 1956, *Lems 2941* (MICH). La Cumbrecita, 1500 m, 9 June 1969, *Bramwell 1878* (LTR; RNG). Same locality, 15 Apr. 1971, *Bramwell & Humphries 3429* (RNG). Same locality, 1000 m, Mar. 1906, *Pitard & Proust 577* (G; L; W). Same locality *Hillebrand* in herb. Christ (Z). Same locality, cliffs above Terena, 13 June 1913, *Sprague & Hutchinson 462* (K). Same locality, north of Los Roques, 1900 m, 22 May 1966, *Lems 7745 b* (MICH). Same locality, rim of Caldera, 22 May 1966, *Lems 7746* (MICH). La Caldera, 1200 m, 25 Mar. 1905, *Pitard & Proust 199* (G; L; P; Z). Garafia, 300 m, 5 June 1936, *Brookes 239* (BM).

Quite common on La Palma on the central, north west and south slopes of the island in La Caldera, La Cumbrecita, Barranco de Angustias, La Cumbre Nueva, Garafia and Pinar de Fuencaliente. Two localities have also been recorded on the east-facing slopes near Puerto de Los Sauces and the Caldereta above Santa Cruz de La Palma.

Most of the localities are in the *Pinus canariensis* forest regions at altitudes of 500–1600 m but recently coastal populations have been collected from open xerophytic *Euphorbia* communities on the dry southern slopes between 50 and 200 m. Geologically the pine forest region consists of an old basement block of syenite and diorite with more recent (Pliocene) coverings of basalt and phonolite. The open xerophytic communities in the south grow on a substratum with a very recent covering of phonolytic lava.

In his account of the Canary Islands Chrysantheminae, Schultz Bipontinus (1844a) described the broad-leaved laurel forest species *A. webbii* from the Island of La Palma, the 'locus classicus' being on one of the eastern-facing slopes of Barranco del Rio. Later collectors, such as Hillebrand (1882), Bornmüller (1901), Pitard (1906) and Sprague & Hutchinson (1923), used the name *A. webbii* on herbarium specimens to refer to a range of populations of another taxon found in the pine forests and lowland *Euphorbia* scrubs of the western, central and southern parts of the island at Las Angustias, La Cumbrecita, Tirajafe and Fuencaliente.

Recent collections by Bramwell in 1969 and Bramwell and Humphries in 1971 from many regions of the island and examination of other herbarium material do in fact show that, within the material thus referred to *A. webbii*, two species can be recognized, differing in habit, leaf shape and cypsela morphology. One of the species, that from the western laurel forest (at Los Tilos), closely agrees in morphology with the type material of *A. webbii* from the Schultz Bipontinus Herbarium at Paris and the Webb Herbarium at Firenze. A photograph of the lectotype is given in Plate 29a. The other more widespread species from the western, central and southern regions of La Palma was previously undescribed. A photograph of the holotype is given in Plate 29b.

A. haouarytheum is morphologically most similar to *A. callichrysum* Svent. from the island of La Gomera. The two species differ in leaf size and shape and cypsela morphology. Table 3 gives a summary of diagnostic characters used to separate them from one another, and from *A. webbii* Schultz Bip.

TABLE 3

Comparison of morphological characters of *A. webbii* Schultz Bip., *A. haouarytheum* Humphries & Bramwell, and *A. callichrysum* (Svent.) C. J. Humphries.

	A. webbii	*A. haouarytheum*	*A. callichrysum*
Leaf			
Shape	Pinnatifid to bipinnatifid	Bipinnatisect	Bipinnatisect
Length (cm)	4·0–14·0	5·0–16·0	10·0–15·0
Width (cm)	2·0– 7·0	2·0– 5·0	2·0– 6·0
Leaf lobes			
Primary (cm)	1·0–5·5 × 0·2–1·5, ovate-lanceolate	2·0–6·0 × 0·1–0·4, linear-lanceolate	0·5–5·0 × 0·2–0·6, linear-lanceolate
Secondary (cm)	Regular serrate teeth	0·5–2·0 × 0·1–0·15, linear-lanceolate	Irregular serrate teeth
Ray cypselas			
Size (mm)	5–6 × 3·5–8	3–5 × 2·5–4·5	4–5 × 4–8
Pappus	Marginal to slightly annular	Coroniform, margin dentate	Absent to annular, margin crispate
Disc cypselas			
Size (mm)	3–4 × 2–3	2–4·5 × 1·5–3	3–5 × 1–3
Pappus	Marginal to slightly annular	Coroniform, margin dentate	Coroniform, margin crispate

Both *A. callichrysum* and *A. haouarytheum* generally occupy similar altitudinal ranges (500–1600 m) although several lowland and coastal populations (50–200 m) of the new species have also been collected. The communities in which they occur are quite different. On La Gomera *A. callichrysum* grows in *Erica arborea* heath and in more humid *Laurus azorica* forest. On the more oceanic and higher island of La Palma, however, *A. haouarytheum* grows in predominantly *Pinus canariensis* forest, *Erica arborea* heath in the lower reaches of the forest zone and *Euphorbia balsamifera* communities in coastal areas.

4. ***Argyranthemum foeniculaceum*** (Willd.) Webb ex Schultz Bip. in Webb & Berthel., Phyt. Canar. 2 : 262 (1844). – Pitard & Proust, Îles Canar., Fl. Archipel : 230 (1908). (Text-fig. 2D, 9.)

Pyrethrum foeniculaceum Willd., Enum. Pl. Hort. Berol. : 903 (1809). – Choisy in Buch, Phys. Beschr. Canar. Ins. : 149 (1825), exc. [var.] δ *bipinnatifidum*.

Chrysanthemum foeniculaceum Brouss. ex Willd., loc. cit., *nom. synon.*
Pyrethrum crithmifolium Willd., loc. cit.
Chrysanthemum crithmifolium Brouss. ex Willd., op. cit. : 904 (1809), *nom. synon.*
Pyrethrum anethifolium Willd., op. cit. : 904 (1809).
Chrysanthemum anethifolium Brouss. ex Willd., op. cit. : 904 (1809), *nom. synon.*
Chrysanthemum crithmifolium (Willd.) Buch in Abh. preuss. Akad. Wiss. 1816–1817 : 364, 375 (1819).
Chrysanthemum anethifolium (Willd.) Buch, loc. cit.
Chrysanthemum foeniculaceum (Willd.) Desf., Cat. Pl. Hort. Reg. Paris ed. 3 : 169 (1829). – DC., Prodr. 6 : 66 (1838), excl. [var.] α *verum* quoad descr. et syn. 'Pyrethrum foeniculaceum δ Choisy . . . Pyrethrum foeniculaceum bot. reg. t. 272'. – Masferer in An. Soc. esp. Hist. nat. 10 : 207 (1881) reimpr. ut Rec. Bot. Tenerife : 131 (1881). – Hutch. in Curtis's Bot. Mag. 142 : t. 8644 (1916). – Burchard in Biblthca bot. 98 : 200 (1908). – Ceballos & Ortuño, Veg. Fl. For. Canar. Occid. : 439 (1951).
Argyranthemum foeniculaceum Webb in Webb & Berthel., tom. cit. : t. 93 (1840), *nom. invalid.*
Argyranthemum anethifolium (Willd.) Webb ex Schultz Bip. in Webb & Berthel., tom. cit. : 267 (1844), excl. descr. et tab. cit.
Argyranthemum frutescens var. *crithmifolium* (Willd.) Pitard & Proust, loc. cit., excl. specim. a Tenerife et Palma.

Stems 60–100 cm, procumbent to ascending, branched throughout the plant, glabrous. *Leaves* 3–10 × 1–6·5 cm, ± obovate in outline, bipinnatisect (–tripinnatisect), petiolate, glabrous, glaucous, crowded around the base of the peduncles, the internodes short ; primary lobes 2–8, 0·5–5 × *c.* 0·5 mm, subopposite, acuminate ; secondary lobes 2–10, alternate to subopposite, 2–15 × *c.* 2 mm, acute. *Inflorescence* monocephalic to laxly corymbose with 1–5 capitula ; peduncles up to 20 cm ; bracts 1 or 2, oblong to linear lanceolate, or absent. *Involucre* 10–18 mm in diameter ; bracts in 3 series, the outer ones triangular to obspathulate ; scarious with a fleshy midrib ; inner bracts with an expanded, scarious, hyaline apex. *Ray florets* 16–22 × 4–5 mm, white, the apex obtuse to 2–3-fid ; *disc florets* 3–3·5 mm, the corolla lobes yellow, the tube whitish. *Ray cypselas* (3–) 5–6 × 3–5 mm, trigonous, arcuate, 2–3-winged, with 2 wide lateral wings and 1 small cuneiform ventral wing ; pappus coroniform, dimidiate on the dorsal edges, dentate ; *disc cypselas* 2–3 × 1–2 mm, obconical, laterally compressed to ± quadrangular, usually with 1 small ventral wing, arcuate in outer series ; pappus coroniform, dentate. *Flowering period:* February to September.

Tenerife: Broussonet in herb. Willdenow 16200 (B, holotypus ; RNG, phototypus). Ladera de Santa Ursula, 600 m, 5 May 1933, *Asplund 1118* (C ; K). Madre del Aguamansa, Orotava valley, 16 July 1845, *Webb 818* (FI). Guimar, 600–700 m, 8 June 1901, *Bornmüller 2469* (G ; P ; W ; Z). Same locality, 1020 m, in lava flow, 9 July 1956, *Lems 2789* (MICH). Same locality, *Perraudière* (P ; S). Same locality 25 Apr. 1855, *Perraudière* (P). Anavigo, 26 May 1855, *Bourgeau 1403* (C ; FI ; G ; K ; P ; Z). Same locality, 6 May 1855, *Bourgeau* in herb. Willkomm (L). Bco. Badajoz, 600 m, 26 Apr. 1933, *Asplund 969* (G). Same locality, 6 July 1894, *Murray* in herb. Gelert (BM ; CGE ; G ; K). Same locality, *Murray* (K ; RHS). Taorem, La Florida, La Resbala, 200 m, Webb (FI). Tamaimo, Hoya de Malpais, 450 m, 5 Mar. 1969, *Bramwell 900* (RNG). Risco Blanco, 600 m, 12 Jan. 1969, *Bramwell 516* (CGE ; RNG). Between Tamaimo and Chio, 800 m, *Lems*

6468 (MICH). El Retamar, 4 Apr. 1971, *Bramwell & Humphries 3262* (BM; RNG). Bco. and saddle between Santiago del Teide and Teno Alto, 23 July 1956, *Lems 2880* (MICH). Pico de Chierfe above Masca, 1100 m, 11 Feb. 1969, *Bramwell 665* (CGE; RNG). Pico de Chierfe, 1000 m, 12 Jan. 1969, *Bramwell 514* (RNG). La Fortelaza de Masca, 1100 m, May 1923, *Burchard 107* (CGE; G; Z). Bco. de Masca, 19 Apr. 1971, *Bramwell & Humphries 3469* (BM; RNG). Masca trail, 800–1000 m, 4 Apr. 1966, *Lems 7377* (MICH). Bco. de Masca, 26 Apr. 1969, *Bramwell 1400* (RNG). Mountains of Teno, Bco. de la Cueva, 200 m, 19 Feb. 1969, *Bramwell* 738 (RNG). May 1845, *Bourgeau 64* (BM; CGE; FI; G; P; W; Z). *Broussonet* (G-DC). *Christian Smith* (C). Herb. Willdenow 16201 (B; RNG). El Pico, *Broussonet* in herb. Willdenow (B; BM; RNG). *Broussonet* in herb. Shuttleworth (BM).

Quite common locally on Tenerife with a disjunct distribution between two main areas: the high cliffs above Ladera de Guimar and Orotava; the cliffs of the south-west facing barrancos of Teno, Masca, Tamaimo and Barranco del Infierno on the western coast (Fig. 9). It is found as a cliff chasmophyte of arid barrancos between 200 and 1100 m, and normally restricted to basal rocks of Miocene or plateau (Pliocene) basalts, although several populations have been collected from areas covered by recent phonolytic lavas.

This species is easily distinguished from other species in the field by the candelabra branching pattern (Fig. 1) and the deeply pinnatisect glaucous foliage. The internodes are extremely short on most specimens, giving new leaves a crowded appearance at the base of the peduncles. The lower leaves are caducous after one season's growth leaving the stem bases quite bare. There is considerable variation in height and habit with generally taller individuals with longer leaves and wider capitula found in the central cliff localities above Guimar and the Orotava valley. Populations from north-west Tenerife have smaller plants with shorter leaves and smaller capitula generally growing at lower altitudes and in a hotter drier climate. It is impossible to distinguish between the two major population groups on any statistical basis so infraspecific ranking is withheld in this treatment.

5. ***Argyranthemum gracile*** Schultz Bip. in Webb & Berthel., Phyt. Canar. 2: 261 (1844). (Text-fig. 2E, 3a, b, 12.)

Pyrethrum foeniculaceum sensu S. Edwards, Bot. Reg. 4: t. 272 (1818), non Willd.

Pyrethrum foeniculaceum [var.] δ *bipinnatifidum* Choisy in Buch, Phys. Beschr. Canar. Ins.: 149 (1825).

Chrysanthemum foeniculaceum [var.] α *verum* DC., Prodr. 6: 66 (1838), quoad descr.

Chrysanthemum foeniculaceum [var.] γ *bipinnatifidum* (Choisy) DC., loc. cit., excl. descr. et syn. Willd.

Argyranthemum frutescens [var.] β *gracile* Webb in Webb & Berthel., tom. cit.: t. 91 (1840), *nom. invalid.*

Chrysanthemum gracile (Schultz Bip.) Masferer in An. Soc. esp. Hist. nat. 10: 207 (1881) reimpr. ut Rec. Bot. Tenerife: 131 (1881). – Burchard in Biblthca bot. 98: 199 (1929), quoad specim. a Arona, Adeje et Guia. – Ceballos & Ortuño, Veg. Fl. For. Canar. Occid.: 439 (1951), quoad specim. a Arona, San Juan et Adeje.

Stems up to 120 cm, ascending, slender, sparsely branched towards the apex to branched throughout, glabrous. *Leaves* 2–10 cm, usually trifid, pinnatisect, petiolate, glabrous ; lobes 2, very rarely 4–6, alternate, 2–4·5 × *c.* 0·4 cm, acuminate ; frequently clusters of 3–4 young leaves are present in the axils of cauline leaves. *Inflorescence* laxly corymbose with up to 50 capitula ; peduncles 20 cm ; bracts leaf-like, trifid to linear lanceolate in outline. *Involucre* 6–12 mm in diameter ; bracts in 3 series ; outer bracts triangular, with narrow, scarious margin and fleshy midrib ; inner bracts obspathulate, with expanded, hyaline, scarious apices. *Ray florets* 10–14 × 3–4 mm, white, 1–3-fid at apex ; *disc florets c.* 3 mm, the corolla lobes yellow, the tube whitish. *Ray cypselas* (3·5–) 4–5 × 2–4 mm, trigonous, arcuate, 3-winged, with 2 broad lateral wings and 1 small cuneiform ventral wing ; pappus coroniform, dimidiate on the dorsal edge, secund on the ventral edge ; *disc cypselas* 2–4 × (1–) 2–3 mm, obconical, compressed, the outer series arcuate, usually with one ventral wing, pappus coroniform. *Flowering period:* February to September.

Tenerife: in rupestribus regionis inferioris insulae Tenerifae in convallis praesertim calioribus orae suae meridionalis las Bandas del Sud dictae, *Webb* in herb. Schultz Bip. (P, lectotype). Chio, Dec. 1968, *Bramwell 416* (RNG). Tamaimo, Riscos del Malpais, 23 Mar. 1969, *Bramwell & Humphries 3260* (BM ; RNG). Between Tamaimo and Chio, 4 Apr. 1971, *Bramwell 275* (RNG). Between Tamaimo and Santiago, 4 Apr. 1971, *Bramwell & Humphries 3268* (RNG). Western slope from Tamaimo to Chio, 800 m, 20 Sept. 1965, *Lems* (MICH). Santiago, 16 Mar. 1888, *Kunze* (K). Same locality, 1 June 1963, *Landbøhojsk 300* (C). Chigerque, north of Guia de Isora, 500 m, 3 May 1857, *Larsen* (C). Same locality, 600 m (Cult. No. 85),

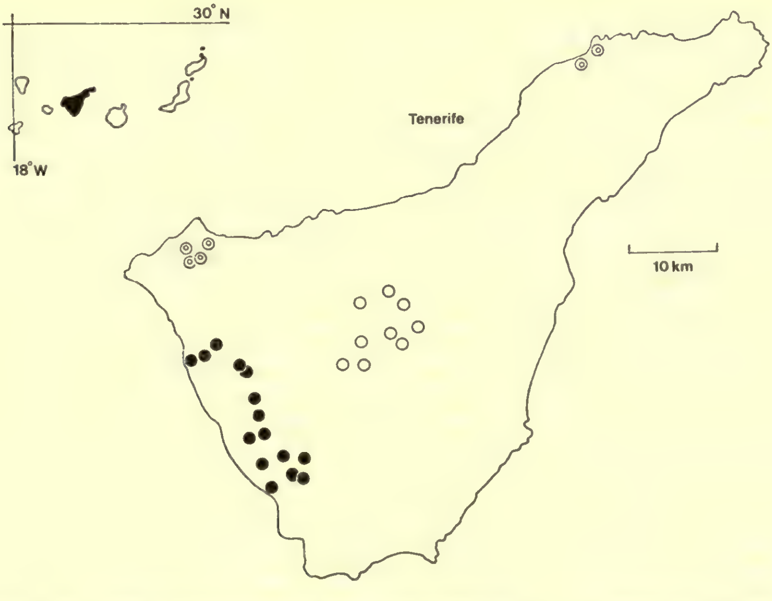

FIG. 12. Distribution of *Argyranthemum gracile* (●), *A. tenerifae* (○) and *A. coronopifolium* (◎) on Tenerife.

27 July 1959, *Larsen* (C). Same locality, 700 m (Cult. No. 87), 27 July 1959, *Larsen* (C). Puerto de San Juan, *Lowe* (BM). 26 June 1855, *Bourgeau 1401* (C; FI; G; K; P; W; Z). Valle Seco, 600 m, 10 Mar. 1969, *Bramwell 948* (CGE; RNG). Same locality, 4 Apr. 1971, *Bramwell & Humphries 3252* (RNG). Same locality, 200 m, Mar. 1925, *Burchard 205* (CGE; G; S; Z). Bco. del Infierno, 25 Aug. 1965, *Lems 5739, 5759* (MICH). Valle de Barriques, 28 June 1855, *Perraudière* (P). Same locality, 6 June 1855, *Perraudière* (P). Same locality, 27 June 1855, *Perraudière* (P). 500 m, March 1855, *Perraudière* (G; P). Same locality, *Webb 1025* (FI). Las Callictus, April 1906, *Pitard* (P). 1857, *Bolle 227* (P). *Broussonet* (C; Z). *Broussonet* (G-DC). 1826, *Christian Smith* (CGE). *Scheele* in herb. Schultz Bip. (P). *Cult. hort. Paris.* 1835 in herb. Webb (FI). *Broussonet* in herb. Webb (FI).

Frequent on the south-west coast of Tenerife from Tamaimo in the north to Adeje in the south (Fig. 12).

Locally dominant component of the xerophytic zone between 100 and 550 m. It has also extended to the lower reaches of the pine forest zone in north-east populations. The basal rocks consist of young (Pliocene and later) phonolytic lavas and plateau basalt.

Morphologically this species most resembles *A. frutescens* subsp. *gracilescens*. There are, however, fewer vegetative branches, the habit is taller and the glabrous, trisect leaves are readily distinguished from the scabridulous pinnatisect leaves of that subspecies. A distinct geographical gap, without any overlap, occurs between these two taxa along the south-east coast of Tenerife near Los Christianos and they can rarely be confused in the field.

6. ***Argyranthemum tenerifae*** C. J. Humphries, sp. nov. (Text-fig. 2F, 12.)

Argyranthemum anethifolium Webb in Webb & Berthel., Phyt. Canar. 2: t. 94 (1840), *nom. invalid.*

Argyranthemum anethifolium Webb ex Schultz Bip. in Webb & Berthel., tom. cit.: 267 (1844), pro parte, non *Pyrethrum anethifolium* Willd. – Pitard & Proust, Îles Canar., Fl. Archipel: 230 (1908).

Chrysanthemum anethifolium sensu Masferer in An. Soc. esp. Hist. nat. 10: 207 (1881) reimpr. ut Rec. Bot. Tenerife: 131 (1881), non Buch. – Burchard in Biblthca bot. 98: 200 (1929), excl. specim. a Cumbre de Bolico. – Ceballos & Ortuño, Veg. Fl. For. Canar. Occid.: 440 (1951).

Ab aliis speciebus sectionis *Argyranthemi* morphologia eius cypselorum et habitu nanophyto, petiolis latis et bracteis triangularis involucri differt.

Caules 30–50 cm, ascendentes, ramosi e basi, glabri vel scabri. *Folia* 2–6 × 0·3–1·6 cm, ovata vel oblonga, pinnatisecta vel bipinnatisecta, glabra vel scabra, petiolus expansus in rhachim longam lateribus parallelibus; lobi primarii 4–10, 0·5–1·6 × 0·1–0·8 cm, oppositi, lobi secundarii 2–16, 2–6 × 0·5–0·8 mm, alterni vel sub-oppositi, acuminati. *Inflorescentia* corymbosus 1–12 capitulis; pedunculi usque ad 30 cm longi; bracteae foliiformes ad lineo-lanceolatae plerumque sessiles ad breviter petiolos. *Involucrum* 7–15 mm diametro, bracteae series 3, bracteae serierum extinarum triangulares, scariosae, costa carnosa, bracteae serierum intimarum lineo-lanceolatae ad lineo-triangulares, acutae, laciniatae, marginibus angustis scariosis. *Radiorum flosculi* albi, ad apicem emarginati vel trifidi ; *discorum flosculi* 3–4 mm longi, lobis corollae flavis et tubis albidis. *Radiorum cypselae* 4–5 × 2·5–5 mm, trigonae, arcuatae, plerumque alis 3, alis duabus lateralibus latis et ala una ventrali cuneiformi, parva ; pappus coroniformis ad marginem dorsalem dimidiatus vel plerumque diminutus et ad instar marginis elevati peripheralis coriacei ; *discorum cypselae* 4–5 × 1·5–2·5 mm, obconicae, teres vel a latere compressae, ala una ventralis cuneiformis vel exalae, pappus coroniformis ad marginem dorsalem dimidiatus in serie externa. *Florescentia* Mars ad Octobrem.

Stems 30–50 cm, ascending, branched from the base, glabrous to scabrous. *Leaves* 2–6 × 0·3–1·6 cm, obovate to oblong in outline, pinnatisect to bipinnatisect, glabrous to scabrous ; the petiole expanded into a long parallel-sided rhachis ; primary lobes 4–10, 0·5–1·6 × 0·1–0·8 cm, opposite ; secondary lobes, 2–16, 2–6 × 0·5–0·8 mm, alternate to subopposite, acuminate. *Inflorescence* corymbose with (1–) 2–12 capitula ; peduncles up to 30 cm ; bracts leaf-like to linear-lanceolate in outline, usually sessile, occasionally shortly petiolate. *Involucre* 7–15 mm in diameter ; bracts in 3 series ; the outer ones triangular, scarious with a fleshy midrib ; the inner ones linear-lanceolate to linear-triangular, acute, laciniate, with narrow, scarious margins. *Ray florets* white, the apex emarginate to 3-fid ; *disc florets* 3–4 mm, the corolla lobes yellow. *Ray cypselas* 4–5 × 2·5–5 mm, trigonous, arcuate, usually 3-winged, with 2 broad lateral wings and 1 small cuneiform ventral wing ; pappus coroniform, dimidiate towards the dorsal edge, often reduced to a coriaceous marginal ridge ; *disc cypselas* 4–5 × 1·5–2·5 mm, obconical, terete to laterally compressed with 1 ventral cuneiform wing or wingless ; pappus coroniform, dimidiate towards the dorsal edge in outer series. *Flowering period* March to October.

Tenerife: below Pico de Teide, 2600 m, 1826, *Berthelot* in herb. Schultz Bip. (FI ; P, holotypus). El Portillo, 2000 m, 22 Oct. 1968, *Bramwell 265, 265(a)* (RNG). Between El Cabezon and El Portillo, 2000 m, 15 Apr. 1969, *Bramwell 1315* (RNG). El Sombrerito, 30 Apr. 1969, *Bramwell 1411* (RNG). Same locality, 10 Apr. 1971, *Bramwell & Humphries 3385* (RNG). Paso de Arenas negras, 30 May 1846, *Bourgeau 849* (BM ; FI ; G ; K ; P). Region de Pico de Teide, 6 July 1855, *Bourgeau* (P). Pico de Teide, 2000 m, 22 July 1963, *Brookes* (BM). 1847, ex herb. Webb (G-DC). Same locality, 6 July 1946, *Ceballos & Ortuño 14424* (MA). 2000 m, 25 Feb. 1935, *Chaytor* (K). Chazua, 5 June 1882, *Hillebrand* in herb. Christ (Z). Same locality, 22 Oct. 1969, *Hansen* (C). Same locality, *de Jussieu* (P). 2000 m, 14 Jan. 1965, *Kaae* (C). 1800 m, 11 May 1957, *Larsen* (C). Montana Blanca, 2900 m, 22 May 1963, *Landbohøjsk* (C). Same locality, 12 Nov. 1965, *Lems 6268* (MICH). Same locality, 11 June 1899, *Murray* (BM). 2200 m, 3 July 1855, *Perraudière* (C ; K ; P ; S). Same locality, 2300 m, 27 Aug. 1839, *Simoniz* (Z).

An obligate chamaephyte in the Cañadas region of Tenerife from El Portillo in the north-east through to Llana de Ucanca and Boca de Tauce in the south.

The sub-alpine scrub habitat is dominated by *Spartocytisus supranubius* and *A. tenerifae* is associated with such species as *Tolpis webbii* and *Descurainia borgaeanum* between 2000 and 2300 m (Fig. 12), on basal rocks which consist entirely of Recent phonolytic lava.

A. tenerifae is the one and only truly alpine species of the genus. The plants are well adapted to the harsh climate of the Cañadas region and die down during the winter for four or five months at a time when the ground is covered with snow. New shoots are produced from short woody ground stems in February and March as the snow clears. The aerial parts of the plants rarely attain a height of more than 50 cm and persist for about six months during the dry summer.

Morphologically it is superficially very similar and frequently confused with the upland montane and pine forest species, *A. adauctum* subsp. *dugourii*, but is easily distinguished, however, by its dwarf habit, the petiolate leaves, the 3-winged ray cypselas and the coroniform pappus.

Argyranthemum tenerifae is usually known as *Chrysanthemum anethifolium* Brouss. ex Willd. Willdenow's description of *Pyrethrum anethifolium* (Enum. Hort. Berol. : 904 (1809)) was based on specimens collected by Broussonet from Tenerife in 1801. These specimens are clearly conspecific with *Pyrethrum foeniculaceum* Willd., (*Argyranthemum foeniculaceum* (Willd.) Webb ex Schultz Bip.), a narrow-leaved chasmophyte from the lower cliffs of Tenerife that is a distinct species.

The plate and description of *A. anethifolium* Webb ex Schultz Bip. in the Phytographia Canariensis refer to *A. tenerifae* but the name is based on *Pyrethrum anethifolium* Willd., which is cited in the synonomy of Schultz Bipontinus's account. As no valid name has ever been applied to this species it is described here as new.

7. ***Argyranthemum maderense*** (D. Don) C. J. Humphries, comb. nov. (Text-fig. 2G, 13.)

Ismelia maderensis D. Don in Sweet, Brit. Flow. Garden. ser. 2, 4 : t. 342 (1836).
Argyranthemum ochroleucum Webb in Webb & Berthel., Phyt. Canar. 2 : t. 96 (1840), *nom. invalid.*
Argyranthemum ochroleucum Webb ex Schultz Bip. in Webb & Berthel., tom. cit. : 259 (1844). – Pitard & Proust, Îles Canar., Fl. Archipel. : 229 (1908).
Chrysanthemum ochroleucum (Webb ex Schultz Bip.) Masf. in An. Soc. esp. Hist. Nat. 10 : 208 (1881) reimpr. ut Rec. Bot. Tenerife : 132 (1881). – Turrill in Curtis's bot. Mag. 166 : t. 67 (1949).

Stems 40–70 cm, procumbent to ascending, slender, branched throughout, glabrous. *Leaves* 2·5–8 × 1–3 cm, obspathulate to obovate, pinnatilobed, ± sessile to shortly petiolate, cuneate at the base, glabrous, dark green, sometimes glaucous ; lobes 2–6, 0·5–3 × 0·4–0·8 cm, serrate, obtuse. *Inflorescence* subcorymbose ; peduncles 5–24 mm ; bracts resembling the leaves to oblong-lanceolate, entire. *Involucre* 11–15 mm ; bracts in 3 series, the outer ones triangular to obovate, scarious, fleshy towards the midrib, the inner ones obspathulate with an expanded, scarious, hyaline apex. *Ray florets* 18–25 × 4–5 mm, pale yellow, the apex emarginate to 3-fid ; *disc florets* 3–3·5 mm, the corolla lobes yellow, the tube white, hyaline. *Ray cypselas* 3–5 × 2–4·2 mm, trigonous, arcuate, 3-winged ; the lateral wings expanded, coriaceous, with a convex dorsal surface, the ventral wing obtriangular, smaller than the lateral wings ; pappus coroniform, dimidiate on the dorsal edge, laciniate ; *disc cypselas* 3–4 × 0·5–2 mm, obconical, laterally compressed, arcuate in the outer series, wingless or 1-winged, irregularly ribbed; pappus coroniform, laciniate. *Flowering period:* January to May.

Lanzarote: Yerva de Santa Maria, in rupibus apricis oppiduli Sancti Bartholomaea, *Webb* in herb. Schultz Bip. (P). Haria, 1845, *Bourgeau 303* (BM; FI; G; K; P; TCD; W; Z). Same locality, 350 m, Apr. 1924, *Burchard 275* (CGE; G; Z). Same locality, Mar. 1922, *Burchard 377* (K; W). Same locality, *Lowe 94* (K). Same locality, 5 Mar. 1905, *Pitard 194* (G; L; P; Z). 'Ye', 14 May 1902, *Murray* (K). Same locality, 26 May 1892, *Murray* (BM; K; RHS). Riscos de Famara, 300 m, 15 May 1969, *Bramwell 1653a* (RNG). Same locality, 350 m, 14 Jan. 1969, *Lems 6601* (MICH). Roque de Famara, 600–625 m, *Lems 6678* (MICH). Same locality, 460 m, *Murray 1902* (K). Yerva de Santa Maria, 21 July 1958, *Murray* (BM). *Lowe* (BM; P).

Endemic to Lanzarote on the north-western coast between Las Rositas and La Caleta above the Playa Famara. Inland localities at La Florida and Yerva de Santa Maria near San Bartholomé have also been recorded (Fig. 13).

It is usually found as an obligate chasmophyte on west-facing cliffs, associated with *Odontospermum* communities. It is restricted to basal rocks composed of Pliocene basalt between 50 and 650 m and on coastal sand dunes in the north-west peninsula.

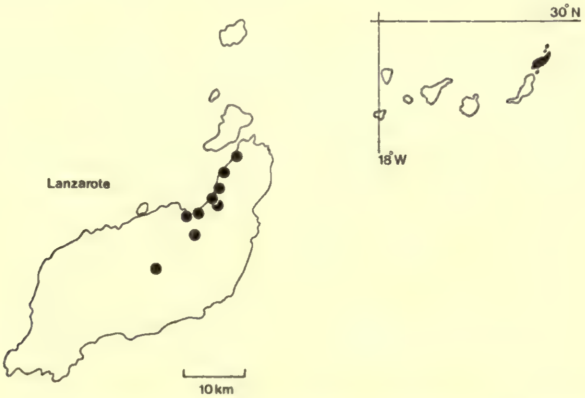

FIG. 13. Distribution of *Argyranthemum maderense* on Lanzarote.

This distinctive species of Lanzarote is usually known as *Argyranthemum ochroleucum* Webb ex Schultz Bip. or *Chrysanthemum ochroleucum* (Webb ex Schultz Bip.) Masf. an epithet coined by Webb to describe its unique yellow ligules for an illustration in the *Phytographia Canariensis*. However, the first description of this species was published under the name *Ismelia maderensis* in 1836 by D. Don in Sweet's *British Flower Garden* with an accompanying illustration drawn from material cultivated at the Chelsea Physic Garden, from seeds originally introduced into Britain by P. B. Webb, from the Canary Islands. D. Don applied the unfortunate epithet '*maderensis*' to the species as he based the diagnosis on a note in one of Webb's earlier manuscripts, '*I. maderensis*, suffruticosa, glauca; foliis sessilibus cuneatis inciso-lobatis; supremis subintegerrimus, capitulis corymbosis, rhachide conica, pappo lobato. Pyrethrum maderense. *Webb MSS'*, which he also cites in the protologue. There is no doubt that, originally, Webb must have mixed up the Lanzarote collections with his Madeiran ones, as the only specimens he is known to have collected of the species are now in the Schultz Bipontinus herbarium in Paris, from gatherings at Yerva de Santa Maria on Lanzarote.

From the description and illustration there is no doubt that D. Don is referring to the Lanzarote endemic and in the absence of any authentic specimens and with the knowledge that the illustration in the protologue was based on live material, the plate is considered to be the holotype.

8. ***Argyranthemum winteri*** (Svent.) C. J. Humphries comb. nov. (Text-fig. 2H, 3c, d, 14.)

Chrysanthemum winteri Svent., Addit. Flor. Canar. 1 : 67, t. 26 (1960).

Chrysanthemum broussonetii sensu Burchard in Biblthca bot. 98 : 201 (1929) pro parte, quoad specim. ex Fuerteventura, non Pers.

Stems 60–80 cm, branched throughout the plant, glabrous. *Leaves* 2–8·5 × 0·6–2·5 cm, oblong ovate to ovate elliptical in outline, bipinnatifid, sessile, glabrous; primary lobes 6–14, opposite to subopposite, 0·3–1·8 × 0·1–0·5 cm, linear-lanceolate, decurrent; secondary lobes dentate, acuminate. *Inflorescence* tightly corymbose, 3–14 capitula; peduncles 2–6 cm; bracts pinnatifid. *Involucre* 14–20 mm; bracts in 3 series, lanceolate to linear-lanceolate in outline; those of the outer series with a fleshy midrib, margins scarious; inner bracts scarious and expanded into a hyaline, laciniate apex. *Ray florets* 10–15 × *c.* 4 mm, white, the apex 2–3-fid; *disc florets* 2–3 mm, the corolla lobes yellow, the tube white. *Ray cypselas* 3–7 × 3·5–7 mm, triquetrous, arcuate, irregularly ribbed, 3-winged;

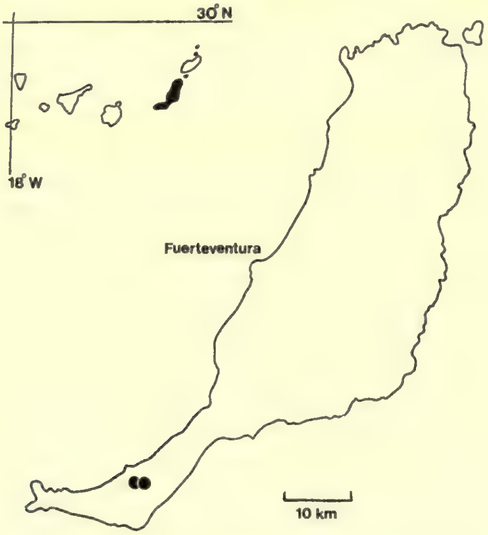

FIG. 14. Distribution of *Argyranthemum winteri* on Fuerteventura.

2 lateral wings prominent, coriaceous, with dentate margins; the ventral wing diminutive, obtriangular; pappus coroniform, dimidiate; *disc cypselas* 5–6 × 1·9–3 mm, claviform, arcuate in the outer series, irregularly 8–10-ribbed, 1-winged, the margins crispate-denticulate; pappus coroniform, lacerate. *Flowering period:* March to April.

Fuerteventura: Handia, Pico de la Zarza, *c.* 800 m, 21 Mar. 1946, *Sventenius* (TENE, holotypus). Same locality, *Sventenius* (TENE). Same locality, 800 m, Apr. 1912, *Burchard* 331 (G; Z). Same locality, 30 Mar. 1971, *Bramwell & Humphries 3175* (BM; RNG). Same locality, 11 Mar. 1967, *Kunkel 10665* (G). Same locality, 650 m, 1 May 1964, *Bramwell* (RNG).

A narrow endemic restricted to the montane regions of Handia (Pico de La Zarza) on Fuerteventura (Fig. 14). It occurs mainly as a chasmophyte in rock fissures of north-west-facing cliffs and occasionally associated with *Odontospermum sericeum* communities around 800 m, on basal rocks of Pliocene 'plateau' basalt.

9. **Argyranthemum lidii** C. J. Humphries sp. nov. (Text-fig. 2I, 15, 16.)

A. broussonetii primo adspectu maxime simile sed cypselis radii trialatis, cypselis disci unialatis, squama indurata versus basin petioli, lobis foliorum acuminatis vel uncinatis, differt.

Caules 50–60 cm, ascendentes, ramosi e basi, plerumque glabri vel aliquando scarbridiusculi. *Folia* 3–9 × 1–3·5 cm, ambitu ovato-elliptica, bipinnatifida, glabra vel scabridiuscula, breviter petiolata; basis petioli tecta squama persistenti incrassata; lobi primarii 6–14, 5–40 × 8–15 mm, subopposititi vel oppositi; lobi secundarii 2–12 × 2–4 mm, dentati, acuminati vel uncinati. *Inflorescentia* corymbosa, 2–6 capitulata, pedunculi 6–10 (–12) cm, glabri vel scabridiusculi; bracteae foliiformes vel pinnatifidae, sessiles plerumque scabridiusculae. *Involucrum* 8–16 mm diametro; bracteae series 3–4 continuas formantibus; bracteae extimae ambitu scariosae ad marginem et carnescentes ad costam; bracteae intimae obspathulatae, ad apicem expansae, scariosae et hyalinae. *Radiorum flosculi* 10–15 × *c.* 4 mm, albi, emarginati vel trifidi ad apicem; *discorum flosculi* 3–3·5 mm, lobis corollae flavis et tubis albidis. *Radiorum cypselae* 3·5–5 × 2–5 mm, trigonae, arcuatae, laeves, trialatae, pappus coroniformis secundus later ventralem cypselae dimidiatus vel absens ad marginem dorsalem; *discorum cypselae* 2·5–4 × 1·3–2·5 mm obconicae a latere compressae vel plus minusve quadrangulares, erectae vel leviter arcuatae ad series extimas, unialatae; pappus coroniformis, dimidiatus ad marginem dorsalem et secundus ad later ventralem seriei extimarum. *Florescentia* Mars ad Aprilem.

Stems 50–60 cm, ascending, branched from the base, usually glabrous, sometimes scabridulous. *Leaves* 3–9 × 1–3·5 cm, ovate-elliptical in outline, bipinnatifid, glabrous to scabridulous, shortly petiolate, the base of the petiole covered with a thick woody scale; primary lobes 6–14, 5–40 × 8–15 mm, subopposite to opposite; secondary lobes 2–12 × 2–4 mm, dentate, acuminate to uncinate. *Inflorescence* corymbose, with 2–6 capitula; peduncles 6–10 (–12) cm glabrous to scabridulous; bracts leaf-like to pinnatifid, sessile, usually scabridulous. *Involucre* 8–16 mm in

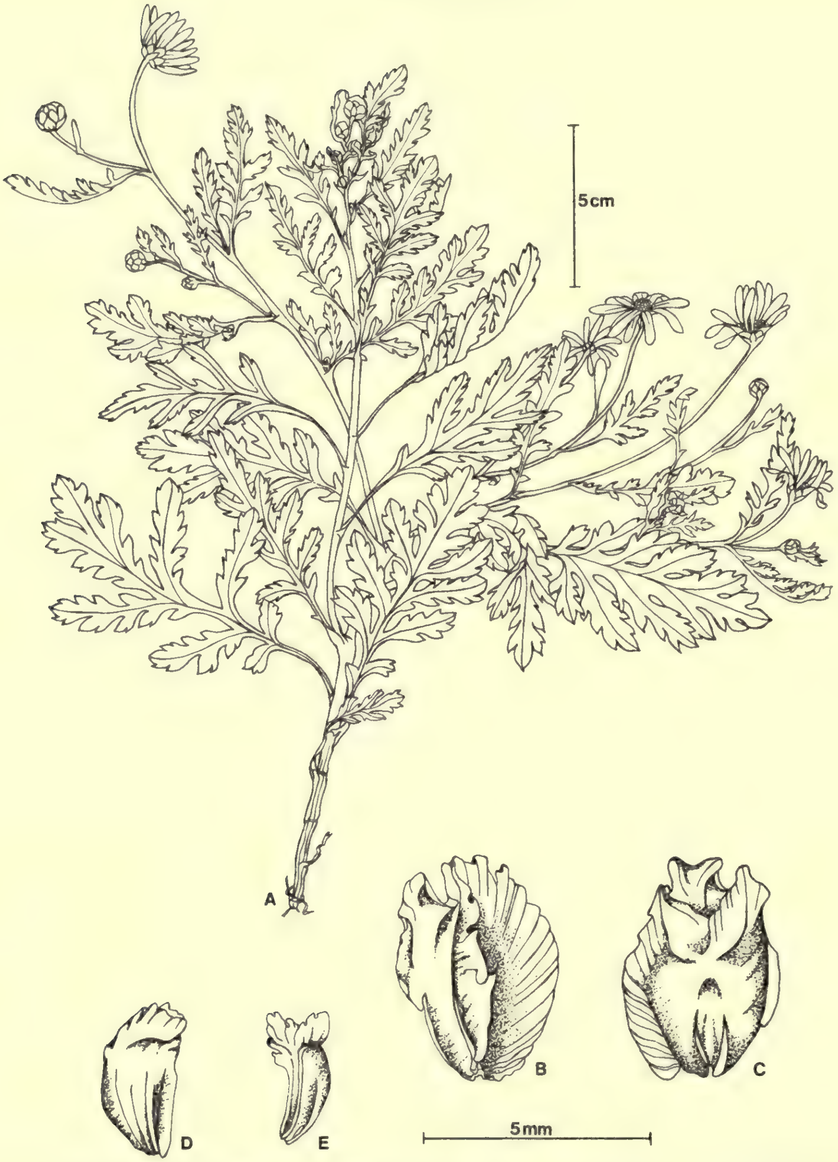

FIG. 15. *Argyranthemum lidii* C. J. Humphries: A, whole plant; B, ventral view, C, dorsal view of ray cypsela; D, lateral view of disc cypsela of outer series; E, lateral view of disc cypsela of inner series.

diameter; bracts in 3 or 4 series; outer bracts scarious at the margins becoming fleshy towards the midrib, scabridulous; inner bracts obspathulate, scarious, hyaline at the margins and apex. *Ray florets* 10–15 × *c.* 4 mm, white, the apex emarginate to 3-fid; *disc florets* 3–3·5 mm, the corolla lobes yellow, the basal tube white. *Ray cypselas* 3·6–5 × 2–5 mm, trigonous, smooth, 3-winged; pappus

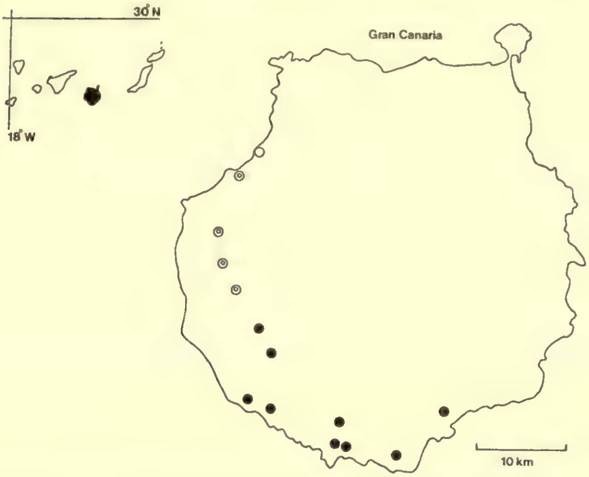

FIG. 16. Distribution of *Argyranthemum lidii* (○), *A. filifolium* (●) and *A. escarrei* (◎) on Gran Canaria.

coroniform, dimidiate, to more or less absent ; *disc cypselas* 2·5–4 × 1·3–2·5 mm, obconical, laterally compressed to more or less quadrangular, erect to slightly arcuate in outer series, 1-winged ; pappus coroniform, dimidiate on the dorsal margin and secund towards the ventral edge of the outer series. *Flowering period:* March to April.

Gran Canaria: Via prope Anden Verde inter Agaete et San Nicolas, 600 m.s.m. Leg. *Bramwell et Humphries 3152.* In herb. Univ. Radingensis servatus (isotypus BM).

This species is named in honour of the late Johannes Lid, for his contributions to the study of phanerogamic plants in the Canary Islands.

An extremely rare species known only from Gran Canaria on the slopes of Risco Faneque along the coast road between Agaete and San Nicolas. It occurs on a rocky substrata consisting of sakalavite and Miocene basalt (Fig. 16).

This species is referable to section *Argyranthemum* on the basis of cypsela morphology. The ray cypselas have large coriaceous lateral wings and a single ventral wing and the disc cypselas have a single cuneiform ventral wing. A coroniform pappus is usually found on both ray and disc cypselas.

The plants occur as low-growing shrubs, branched only from the base. The leaves are quite unlike any other species of this section and are superficially similar to those of *A. broussonetii* or *A. adauctum* subsp. *jacobaeifolium* (Fig. 2I, N, U). Other characteristics for the species are the hard abaxial scales found at the base of the petioles and the uncinate tips on some of the leaf lobes.

The only specimens of this species (*Bramwell & Humphries 3152*) were collected at the bottom of an inaccessible basalt cliff, and the population is suspected to have developed from seeds that have dropped from the top of the cliff – an apparently richly wooded area dominated by conifers.

10. ***Argyranthemum dissectum*** (Lowe) Lowe, Man. Fl. Madeira : 464 (1868). (Text-fig. 2J, 3f, 17.)

Matricaria pinnatifida [var.] β Desrouss. in Lam., Encycl. Méth. 3 : 729 (1792).
Chrysanthemum lacerum Desrouss., loc. cit., *nom. synon.*
Chrysanthemum dissectum Lowe in Trans. Camb. phil. Soc. 6 : 539 (1838).
Argyranthemum pinnatifidum Webb in Webb & Berthel., Phyt. Canar. 2 : t. 95 quoad fig. 2, 4 (1840), *nom. invalid.*
Stigmatotheca lacera Schultz Bip. in Webb & Berthel., tom. cit. : 257 (1844), *nom. superfl.*

Stems 60–120 cm, lax, branched throughout, glabrous. *Leaves* 2–9 × 0·2–3·5 cm, ovate-oblong to lanceolate in outline, bipinnatisect, pectinate, petiolate, glabrous ; primary lobes 10–16, 0·5–2 × *c.* 0·5 cm, subopposite, linear ligulate to narrowly lanceolate, acuminate ; secondary lobes dentate-acuminate. *Inflorescence* more or less corymbose, with 1–5 capitula ; peduncles 10–25 cm, slender ; bracts 1–2, lanceolate, entire. *Involucre* 14–20 mm in diameter ; bracts in 3–4 series, triangular to spathulate in outline ; outer bracts fleshy, with a narrow, scarious margin ; inner bracts scarious, hyaline, expanded at the apex. *Ray florets* 15–22 × *c.* 0·5 mm, white, the apex emarginate to 3-fid ; *disc florets c.* 3 mm, the corolla lobes yellow. *Ray cypselas* 4–5 × 2–3 mm, turbinate, trigonous, unequally 3-winged ; the 2 lateral wings large, coriaceous, laciniate ; the ventral wing diminutive, carinate ; pappus coroniform, dimidiate on the dorsal edge, pointing towards the ventral edge ; *disc cypselas* 3–4 × 2–3 mm, obconical, slightly compressed to terete or ± quadrangular, 1-winged ; pappus coroniform, dimidiate, on the dorsal edge, in a dentate beak or apical aculus on the ventral edge. *Flowering period:* March to May.

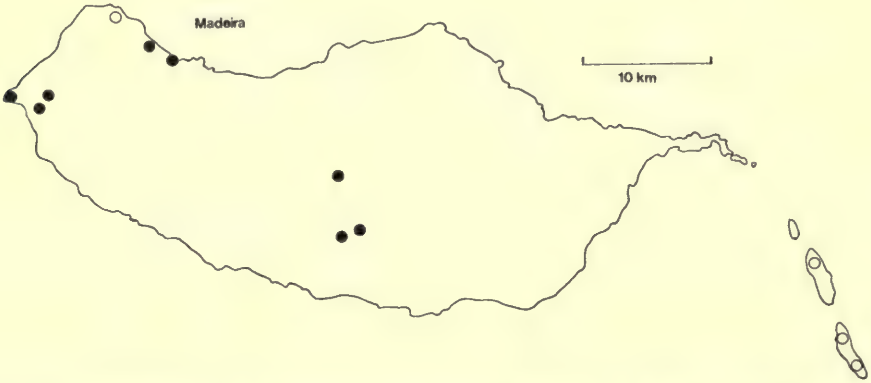

FIG. 17. Distribution of *Argyranthemum dissectum* (●) and *A. haemotomma* (○) on Madeira.

Madeira: Punta Pargo, 15 Apr. 1860, *Lowe* (BM ; G ; K). Same locality, 5 May 1862, *Lowe* (BM). Same locality, 24 Apr. 1838, *Lowe* in herb. Tucker (BM). Same locality, 370 m, 7 June 1865, *Norman* (CGE). Pico Grande, 23 June 1855, *Moriz* (BM). Cabo Girao, at top of cliff, 24 Apr. 1838, *R. Lowe* in herb. Tucker

(BM, lectotype). Same locality, 11 May 1838, *Lowe* in herb. Leman (CGE). Malhada Velha, 1200 m, *Mandon 319* (C; G; K). Riberia Frio, *Vogel* (K). North coast between Seixal and Porto Moniz, 10–25 m, 1 May 1966, *Lems 7637* (MICH). Caninho, 3 Aug. 1902, *Vahl.* (C). 1837, *Leman* (CGE; K). 1839, *Leman* (G). Det. *Webb* in herb. Schultz Bip. (P). 1856, *Mason 335* (CGE).

A rare endemic of moist cliffs, banks and hedges from the north-west peninsula of Madeira between Porto Moniz and Punta Pargo. The species has also been recorded from south-facing cliffs of the Curral das Freiras near Cabo Giram and west-facing cliffs of Pico Grande (Fig. 17).

11. ***Argyranthemum thalassophilum*** (Svent.) C. J. Humphries, comb. et stat. nov. (Text-fig. 2K.)

Chrysanthemum pinnatifidum var. *thalassophilum* Svent. in Indices Sem. Hort. Acclim. Pl. Arautapensi 1968 (4) : 59 (1968), reimpr. ut Pl. Macarones. nov. v. minus cogn. 1 : 17 (1968).

Stems up to 90 cm, ascending, branched throughout, glabrous. *Leaves* 2·4–6 × 0·7–3·5 cm, obovate-trapeziform, pinnatifid to bipinnatifid, petiolate, glabrous; primary lobes 2–6, 0·3–2·5 × 0·2–0·8 cm, opposite to subopposite; secondary lobes 1–7, 0·2–0·5 × *c.* 0·2 cm, alternate, obtuse, sometimes absent. *Inflorescence* corymbose, with 2–6 capitula; peduncles 5–12 cm; bracts pinnatifid to linear-lanceolate, sometimes subtending the capitula. *Involucre* 12–18 mm in diameter; bracts in 3–4 series, triangular to obovate; outer bracts fleshy along the midrib, invested with an obtuse fleshy keel towards the apex; inner bracts scarious, with a flabelliform, rotund-crenulate, hyaline apex and distinct, divergent veins. *Ray florets* 16–20 × 5–8 mm, creamy white, the apex entire or emarginate; *disc florets c.* 4 mm, the corolla lobes yellow, the tube pale yellow or whitish. *Ray cypselas* 4·5–6 × 4·5–8 mm, trigonous, 3-winged, the wings coriaceous; pappus coroniform, dimidiate on dorsal edge and rising to a point on the ventral edge, irregularly dentate; *disc cypselas* 4·2–5·5 × 1–3 mm, obconical, laterally compressed to terete, 1-winged; pappus coroniform, dimidiate on dorsal edge or pointing towards the ventral edge in outer series, irregularly dentate. *Flowering period:* March to April.

Salvage Islands: Grand Piton, rocky places near the sea, 7 May 1953, *Sventenius* (TENE, holotype). Tafira Botanic Garden, ex locus classicus, *Bramwell & Humphries* (RNG).

A conspicuous endemic of coastal rocks between 5 and 10 m on Grand Piton Island.

The putative relationship of *A. thalassophilum* with *A. pinnatifidum* is questionable. *A. thalassophilum* is morphologically distinct as well as geographically isolated from all other taxa within the genus. It differs from *A. pinnatifidum* by the larger coroniform pappus of both the ray and disc cypselas and its distinctive leaf shape (Fig. 2). On the basis of sectional characters it is most like the Canary Islands taxa *A. frutescens* subsp. *succulentum* and subsp. *canariae*, but differs from them by the unique carinae of the outer involucral bracts.

12. ***Argyranthemum callichrysum*** (Svent.) C. J. Humphries, comb. nov. (Text-fig. 2L, 3e, 18.)

Chrysanthemum callichrysum Svent., Addit. Fl. Canar. 1 : 65, t. 25 (1960).

Stems 60–100 cm, erect, branched throughout the plant, glabrous. *Leaves* 10–15 × 2–6 cm, ovate-elliptical in outline, bipinnatisect, petiolate, glabrous, dark green on adaxial surface, pale green on abaxial surface ; primary lobes 6–10, 0·5–5 × 0·2–0·6 cm, subopposite to opposite ; secondary lobes 2–8, alternate, acuminate. *Inflorescence* corymbose, with 3–35 capitula ; peduncles 5–15 cm ; bracts pinnatifid to pinnatisect. *Involucre* 9–14 mm ; bracts in 3 series, triangular-lanceolate to ovate or linear-lanceolate in outline, outer bracts scarious with a fleshy midrib, inner bracts scarious with an expanded apex. *Ray florets* 15–20 × 2–5 mm, yellow or creamy white, the apex entire or 1–3-fid ; *disc florets* *c.* 3 mm, the corolla lobes yellow, *Ray cypselas* 4–5 × 4–8 mm, obconical, trigonous, solitary or with 2–6 coalesced together, with 2–3 diminutive wings with crispate margins ; pappus a narrow marginal ridge to ± coroniform, dimidiate to absent on the dorsal edge ; *disc cypselas* 3–5 × 1–3 mm, obconical to claviform, irregularly 4–5-angled, with a single obtriangular wing ; pappus ± coroniform, crispate on the margins. *Flowering period:* March to June.

La Gomera: Iguelero, 1000 m, 18 May 1946, *Sventenius* (TENE, holotypus). Same locality, *Sventenius* (TENE). Tagamiche, 900 m, 18 Mar. 1966, *Lems 7296* (MICH). Bco. de Argaga, 10–250 m, 23 Mar. 1966, *Lems 7321* (MICH). Between Agando and Iguelero, 27 June 1969, *Bramwell & Humphries 3174* (RNG). Roque Agando, 1150 m, 19 Mar. 1966, *Lems 7240* (MICH).

Sparsely distributed from Barranco de Argaga on the south-west coast to the south and south-facing slopes of the central mountains of Igualero, Agando and Tagamiche. A single locality is also recorded from Vallehermoso on the north-west coast (Fig. 18).

A. callichrysum is associated with xerophytic scrub vegetation on rocky slopes. At lower altitudes it grows on cliffs in *Euphorbia regis-jubae* communities between 10 and 250 m and at higher altitudes it usually occurs as scattered individuals in

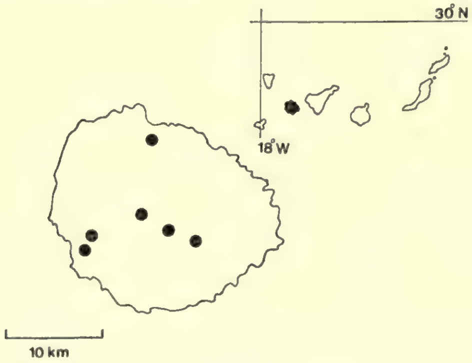

FIG. 18. Distribution of *Argyranthemum callichrysum* on La Gomera.

the *Juniperus phoenicea* scrub and *Erica arborea* communities between 900 and 1200 m. The basal rocks consist of trachyphonolytes and basalts.

The plants of Igualero have mostly yellow ligules but in all other populations they are creamy white. The montane populations are morphologically most similar to *A. haouarytheum* and occupy similar altitudinal ranges (p. 196). However, *A. callichrysum* consistently differs by its more numerous and wider leaf-lobes and the diminutive wings and pappus on the ray cypselas.

13. ***Argyranthemum sventenii*** Humphries & Aldridge, sp. nov. (Text-fig. 2W, 19, 23.)

Similis *A. callichryso* (Svent.) C. J. Humphries sed foliis parvis cum lobis angustis dissectis minoribus, involucris multo angustioribus et flosculis radiorum perpusillis differt.

Caules 30–60 cm, basi ramosi, glabri. *Folia* 3–10 × 1–6 cm, ambitu obovata, pinnatisecta vel bipinnatisecta, petiolata, glabra; lobi primarii 3–10, 0·5–3 × 0·05–0·3 cm, lineo-lanceolati, oppositi vel suboppositi; lobi secundarii 1 vel 2, 0·1–0·5 × *c.* 0·05 cm, alterni, acuti. *Inflorescentia* corymbosa, 10–25 capitulata; pedunculi 5–9 cm, bracteae foliiformes vel lineo-lanceolateae. *Involucrum* 6–11 mm diametro; bracteae series 3 formantes, bracteae extimae ambitu anguste triangularis scariosae, bracteae intimae anguste obovatae vel lineo-lanceolati, hyalinae ad marginem et laciniatae ad apicem. *Radiorum flosculi* 6–10 × *c.* 2 mm, eburnei, integri vel emarginati ad apicem, *discorum flosculi c.* 4 mm longi, lobis corollae flavis et tubis albis. *Cypselae radiorum* 3–4 × 3–5·5 mm, turbinatae, trigonae, 3–4 alatae, binae vel ternae saepe coalescentes; pappus anguste coroniformis, irregulariter dentatus; *discorum cypselae* 2·5–4 × 1·5–2·8 mm, a latere compressae vel teretes, plerumque unialatae; pappus coroniformis, irregulariter dentatus. *Florescentia* Januarius usque Mars.

Stems 30–60 cm, branched at the base, glabrous. *Leaves* 3–10 × 1–6 cm, obovate pinnatisect or bipinnatisect, petiolate, glabrous; primary lobes 0·5–3 × 0·05–0·3 cm, linear-lanceolate; secondary lobes 1 or 2, 0·1–0·5 × *c.* 0·05 cm, alternate, acute. *Inflorescence* corymbose with 10–25 capitula; peduncles 5–9 cm; bracts leaf-like to linear-lanceolate. *Involucre* 6–11 mm in diameter; bracts in 3 series; outer bracts diminutive, narrowly triangular, scarious; inner bracts narrowly obovate to linear-lanceolate, scarious, hyaline towards the margin, laciniate at the apex. *Ray florets* 6–10 × *c.* 2 mm, creamy white, entire or emarginate at the apex; *disc florets c.* 4 mm with yellow corolla lobes and white tubes. *Ray cypselas* 3–4 × 3–5·5 mm, turbinate, trigonous, 3–4-winged, often coalesced into groups of 2 or 3; pappus narrowly coroniform, irregularly dentate; disc cypselas 2·5–4 × 1·5–2·8 mm, laterally compressed to terete, usually 1-winged; pappus coroniform, irregularly dentate. *Flowering period:* January to March.

Holotypus: Via ad meridiem e San Andrés prope Restigam, leg. 16 Mar. 1973, *Aldridge 1293*. In herb. Univ. Radingensis servatus (RNG).

A rare species occurring as a single population in the *Euphorbia balsamifera–Kleinia neriifolia* lowland xerophytic scrub near Restiga on the central slopes of the South Hierro peninsula.

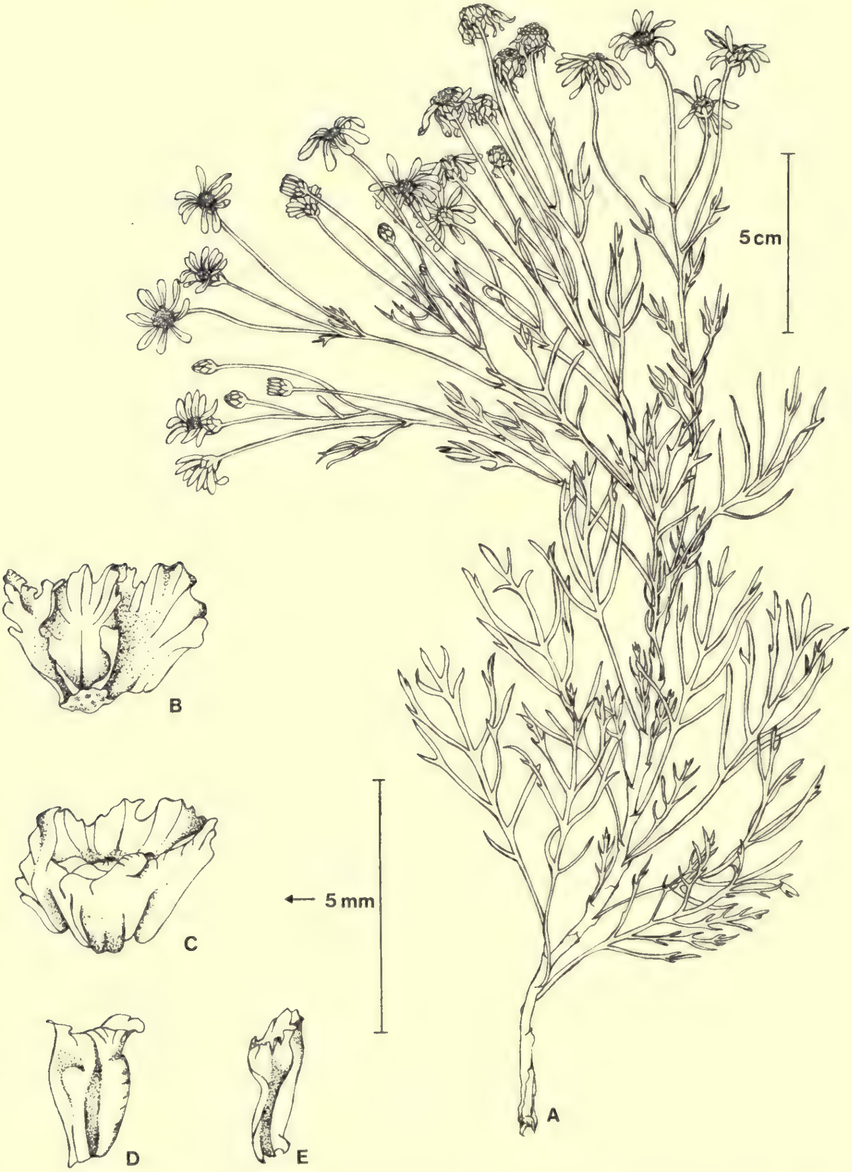

FIG. 19. *Argyranthemum sventenii* Humphries & Aldridge : A, whole plant ; B, ventral view, C, dorsal view of ray cypsela ; D, lateral view of disc cypsela of outer series ; E, lateral view of disc cypsela of inner series.

Recent collections by Miss A. Aldridge (1973) from various regions of Hierro indicate that three species occur on the island. *A. hierrense* and *A. canariense* occur in the laurel forests on the northern slopes, but this is the first collection to be obtained in the south.

The ray-cypsela morphology of these plants most closely resembles that of *A. callichrysum*, in that the wings and pappus are very reduced and the pericarp is often coalesced to form groups of 2 or more cypselas. The plants can readily be distinguished from *A. callichrysum* by their small pinnatisect or bipinnatisect leaves, and tiny capitula. The species can also be distinguished from other members of section *Argyranthemum* occurring in the lowland xerophytic zones of the western Canary Islands (i.e. *A. frutescens* and *A. gracile*) by the leaf shape (Fig. 2).

Section 2. ***SPHENISMELIA*** (Schultz Bip.) C. J. Humphries

ARGYRANTHEMUM sect. SPHENISMELIA (Schultz Bip.) C. J. Humphries, comb. nov.

Ismelia sect. *Sphenismelia* Schultz Bip. in Webb & Berthel., Phyt. Canar., 2 : 272 (1844).
Ismelia sect. *Grammismelia* Schultz Bip. in Webb & Berthel., loc. cit.

Plants glabrous or hispid only on the leaf midribs. *Leaves* bipinnatifid to bipinnatisect, petiolate. *Ray florets* wingless to 1–2 (–3)-winged ; the wings narrow, scarious ; pappus coroniform. *Disc cypselas* obconical, laterally compressed with usually 2 or rarely 1 coriaceous wings ; pappus coroniform.

14. ***Argyranthemum coronopifolium*** (Willd.) C. J. Humphries, comb. nov. (Text-fig. 2M, 12.)

Pyrethrum coronopifolium Willd., Enum. Hort. Berol. : 904 (1809).
Chrysanthemum grandiflorum [var.] δ *cuneiforme* DC., Prodr. 6 : 66 (1838).
Chrysanthemum broussonetii [var.] β *parviflorum* DC., tom. cit. : 67 (1838).
Argyranthemum frutescens [var.] δ *cuneiforme* Webb & Berthel., Phyt. Canar. 2 : t. 92 fig. sinistr. (1839), *nom. invalid.*
Chrysanthemum grandiflorum [var.] γ [sphalm. pro δ] *coronopifolium* (Willd.) Steudel, Nomencl. Bot. ed. 2, 1 : 357 (1840).
Chrysanthemum coronopifolium (Willd.) Steudel, tom. cit. : 356 (1840), *nom. synon.*
Ismelia coronopifolia (Willd.) Schultz Bip. in Webb & Berthel., tom. cit. : 272 (1844). – Pitard & Proust, Îles Canar., Fl. Archipel. : 232 (1908) quoad specim. a Tenerife.
Argyranthemum coronopifolium (Willd.) Webb ex Schultz Bip. in Webb & Berthel. loc. cit., *nom. synon.*
Chrysanthemum coronopifolium (Willd.) Masf. in An. Soc. esp. Hist. nat. 10 : 208 (1881), reimpr. ut Rec. Bot. Tenerife : 132 (1881), excl. spec. a Orotava et Gran Canaria, non *C. coronopifolium* Vill. (1788). – Burchard in Biblthca bot. 98 : 201 (1929), excl. specim. a Ferro. – Ceballos & Ortuño, Veg. Fl. For. Canar. Occid. : 441 (1951), quoad specim. a Tenerife.

Stems 40–120 cm, prostrate, procumbent or ascending, branched throughout the plant, glabrous. *Leaves* 1·5–9 × 0·5–4·5 cm, obovate to obspathulate, 1–2-pinnatilobed, glabrous ; the petioles cuneate ; primary lobes 2–8, 0·5–3·5 × 0·3–1·5 cm, opposite to subopposite, secondary lobes 2–5, alternate, dentate, obtuse to acute. *Inflorescence* monocephalic to corymbose, with 1–8 capitula ; peduncles up to 20 cm long ; bracts 1 or 2, or often absent, linear-lanceolate in outline. *Involucre* 12–22 mm ; bracts in 3 series ; outer bracts triangular in outline, scarious, with a thick fleshy midrib ; inner bracts obovate to oblong, scarious, with an expanded hyaline apex. *Ray florets* 11–24 × *c.* 6 mm, white, the apex emarginate to 3-fid ; *disc florets* 3–4 mm, the corolla lobes yellow, the tube pale yellow or white, hyaline. *Ray cypselas* 5–7 × 3–6 mm, trigonous, arcuate, 1–3 (–4)-winged ; pappus coroniform ; *disc cypselas* 3–4 × 1·5–3 mm, obconical, turbinate, arcuate in outer series, laterally compressed to ± quadrangular, usually with 2 wings, rarely 1 wing or wingless ; pappus coroniform dimidiate or absent on the dorsal margin. *Flowering period:* March to November.

Tenerife: In herb. bot. Berol., *Willdenow 16203* (B, holotype ; RNG, phototype). Roque del Fraile, Buenavista, Teno, 70 m, 3 Nov. 1968, *Bramwell 318* (RNG). Same locality, *Bramwell 553* (RNG). Same locality, 25 Jan. 1969, *Bramwell 556* (RNG). Same locality, 100 m, 13 July 1969, *Bramwell & Humphries 3271* (BM ; RNG). Same locality, 19 June 1855, *Bourgeau* (FI ; P). Same locality, 300 m, May 1923, *Burchard 174* (G ; Z). Same locality, 200 m, in scrub vegetation, 29 Mar. 1960, *Larsen* (C). Same locality, 19 June 1956, *Lems 2634* (MICH). Same locality, 220 m, 9 Oct. 1965, *Lems 6094* (MICH). Same locality, *Webb* (FI). Bajamar, in herb. Schultz Bip. (P). Same locality, in herb. Webb 196 (FI). Cultivar No. 13 (G-DC). In herb. de Jussieu (P). In herb. Webb (P).

A. frutescens (L) Webb ex Schultz Bip. × *A. coronopifolium* hybrids ; El Fraile, 3 Nov. 1968, *Bramwell 319* (RNG). Same locality, 13 Feb. 1969, *Bramwell 690* (RNG). Mirador Pompeii, 5 Apr. 1971, *Bramwell & Humphries 3280* (RNG). Same locality, 21 Oct. 1969, *Hansen* (C).

A rare endemic of Tenerife from the north-facing slopes of the Teno promontory at Buenavista. It is also recorded from localities around Bajamar on the north coast of the Anaga peninsula, from specimens in the herbarium of P. B. Webb, but it is likely that the species is extinct in this region today.

It is now a rare chasmophyte of wet, north-facing cliffs, commonly associated with stem succulents of the association *Aeonio–Euphorbetum canariense* Rivas & Esteve ; 50–300 m. The basal rock consists of plateau (Pliocene) basalts.

A large, complex hybrid swarm with many intermediates has developed between *A. coronopifolium* and *A. frutescens* subsp. *frutescens* on the scree slopes formed by the construction of a tunnel in 1965 through the cliffs at El Fraile connecting Buenavista with the Punta de Teno. Hybrid backcrosses to *A. coronopifolium* are rapidly being produced causing grave threats to the survival of the rare parental populations (Humphries, 1973).

15. ***Argyranthemum broussonetii*** (Pers.) C. J. Humphries, comb. nov. (Text-fig. 3j, l, 20.)

Chrysanthemum broussonetii Pers., Syn. Pl. 2 : 461 (1807). – Balbis, Cat. Hort. Taurin. : 20 (1810). – DC., Prodr. 6 : 66 (1838), excl. [var.] *β parviflorum*. – Masferer in An. Soc. esp. Hist. nat. 10 : 208 (1881), reimpr. ut Rec. Bot. Tenerife : 132 (1881). – Burchard in Biblthca bot. 98 : 201 (1929), quoad specim. a Tenerife. – Ceballos & Ortuño, Veg. Fl. For. Canar. Occid. : 441 (1951), excl. specim. a Hierro.

Pyrethrum broussonetii Choisy in Buch, Phys. Beschr. Canar. Ins. : 149 (1825).

Argyranthemum pinnatifidum Webb in Webb & Berthel., Phyt. Canar. 2 : t. 95, quoad fig. 3, 5–9 (1840), *nom. invalid.*

Ismelia broussonetii (Choisy) Schultz Bip. in Webb & Berthel., tom. cit. : 274 (1844). – Pitard & Proust, Îles Canar., Fl. Archipel : 232 (1908).

Stems up to 120 cm, procumbent to ascending, branched throughout the plant, glabrous. *Leaves* 3–16 × 0·5–8 cm, obovate-elliptical, bipinnatifid or rarely bipinnatisect, shortly petiolate to ± sessile, glabrous or sparsely hairy on the midrib ; primary lobes 2–18, 0·5–5 × 0·3–2 cm, ovate, opposite to subopposite ; secondary lobes dentate, acuminate. *Inflorescence* corymbose ; peduncles 4–12 cm, stout ; bracts leaf-like to narrowly oblong. *Involucre* 12–22 mm in diameter ; bracts in 3 series ; outer bracts triangular, fleshy ; inner bracts obovate, scarious with an expanded, hyaline apex. *Ray florets* 20–38 × 4–8 mm, white, 1–3-fid at the apex ; *disc florets c.* 4 mm, the corolla lobes yellow, the tubes pale yellow or white. *Ray cypselas* 4–6 × 3–5 mm, obconical, trigonous to ± terete, the wings 1–3 or rarely 4, often wingless ; pappus a large, coriaceous expansion of the pericarp to a marginal ridge, or a cuspate corona to sometimes absent ; *disc cypselas* 3–5 × 2–4 mm, obconical, laterally compressed to ± quadrangular with 2 or rarely 1 wings ; pappus coroniform, sometimes expanded laterally in outer series. *Flowering period:* February to October.

Two subspecies are recognized.

a. subsp. **broussonetii** (Text-fig. 2N 1.)

Argyranthemum pinnatifidum Webb & Berthel., Phyt. Canar. 2 : t. 95 fig. 3, 5–9 (1840), *nom. invalid.*

Stems up to 120 cm, ascending. *Leaves* 3–16 × 0·5–8 cm. *Involucre* 12–22 mm. *Ray cypselas* 5–6 mm. Endemic to Tenerife.

Tenerife: Broussonet in herb. Persoon (L, holotype). Montes de Anaga, Los Pajales, 900 m, 16 May 1933, *Asplund 1305* (G ; K). Same locality, 5 Oct. 1900, *Bornmüller 815* (G), Pico Inglés, 550 m, 2 Aug. 1968, *Bramwell 421* (RNG). Punta de Anaga, 600 m, May 1926, *Burchard 325* (G ; S ; Z). Cumbre de Anaga, 1957, *Lems 3081* (MICH). Same locality, 11 June 1894, *Murray* (G). Same locality, 1890 (BM ; K). Taganana, *Broussonet* in herb. Schultz Bip. (P). 600–800 m, 30 May 1901, *Bornmüller 2466* (P). Vueltas de Taganana, 7 Feb. 1969, *Bramwell 651* (RNG). Same locality, 21 May 1969, *Bramwell 1531* (RNG). Same locality, 1000 m, 3 Mar. 1961, *Hummel* (S). Cruz de Taganana, 900 m, 16 Aug. 1954, *Lems 2199* (MICH). Same locality, 1000 m, Mar. 1855, *Perraudière* (P ; S). 900 m, Feb. 1906, *Pitard & Proust 578* (G ; L ; P). Tegueste, 4 Feb. 1855, *Bourgeau 7405* (B ; C ; FI ; G ; K ; M ; P ; W ; Z). Same locality, 13 Feb. 1855, *Perraudière* (P). Same locality, 2 May 1846, *Webb* (FI). Roque de las Pasas, 934 m, 9 Apr. 1971, *Bramwell & Humphries 3382* (RNG). Valle de Chinamara, Apr. 1907, *Burchard 191* (Z). Tigaige, 7 May 1902, *Murray* (K). Monte Bajamar, 1842, *Webb 544* in herb. Schultz Bip. (P). Same locality, 1856, *Bourgeau 1409* (P). Same locality, Broussonet in herb. Ventenat (G). Same locality 1807, *Broussonet* (G-DC). Same locality, 1820, *Courant* (G-DC). Same locality, 1796, *Ledru* in herb. de Jussieu (P). Same locality, *Mason 2463* (S). *Persoon* (L). Icod el Alto, on the road to Realejos, 650 m, 13 Apr. 1969, *Bramwell 1257* (RNG). Icod de los Vinos, 1 June 1895, *Keugler* (K). Icod el Alto to Tigaiga, 3 Dec. 1965, *Lems 6412* (MICH).

Locally common on the Punta de Anaga, the north-east peninsula of the island, along the central mountains from Las Mercedes to Tegueste on the north coast. Small populations also occur in the Orotava valley between Icod Alto and Realejo (Fig. 20). Predominantly, a subspecies of open clearings of *Laurus azorica* forest between 550 and 1000 m on basal rocks of Miocene and Pliocene plateau basalt.

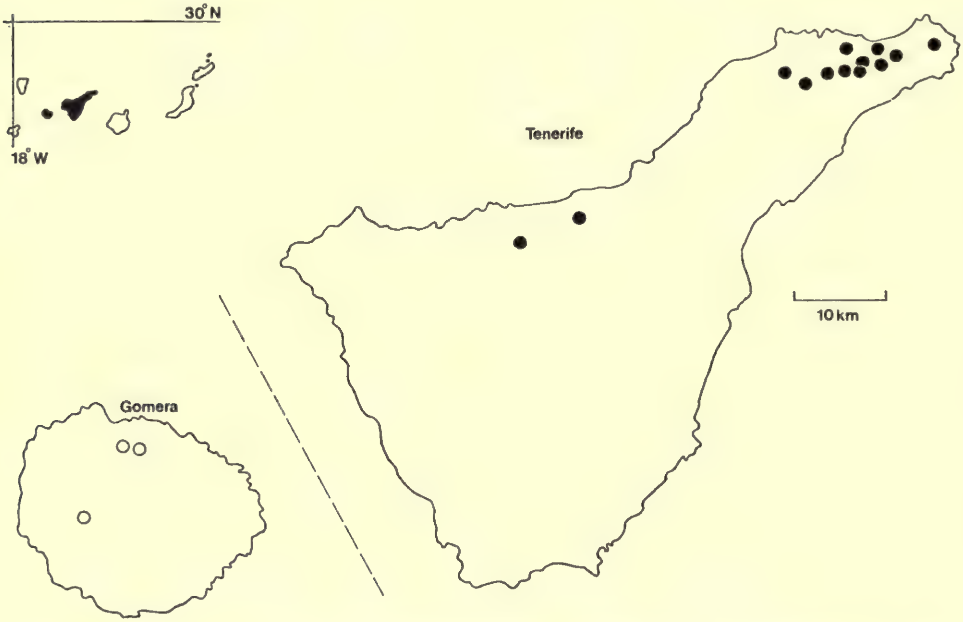

FIG. 20. Distribution of *Argyranthemum broussonetii* subsp. *broussonetii* (●) and subsp. *gomerensis* (○) on Tenerife and La Gomera.

This subspecies is variable throughout its range, particularly in foliage characters. Populations with almost pinnatisect leaves and smaller capitula are common in the Orotava valley. These plants differ from the plants of the Anaga peninsula with broader leaves and larger capitula but are not really worthy of taxonomic distinction as many intermediate forms exist.

b. subsp. ***gomerensis*** C. J. Humphries, subsp. nov. (Text-fig. 2N 2, 20, 21.)

A subspecie *broussonetii* habitu tenuior, floribus saepius parvis, cypselis parvioribus differt.

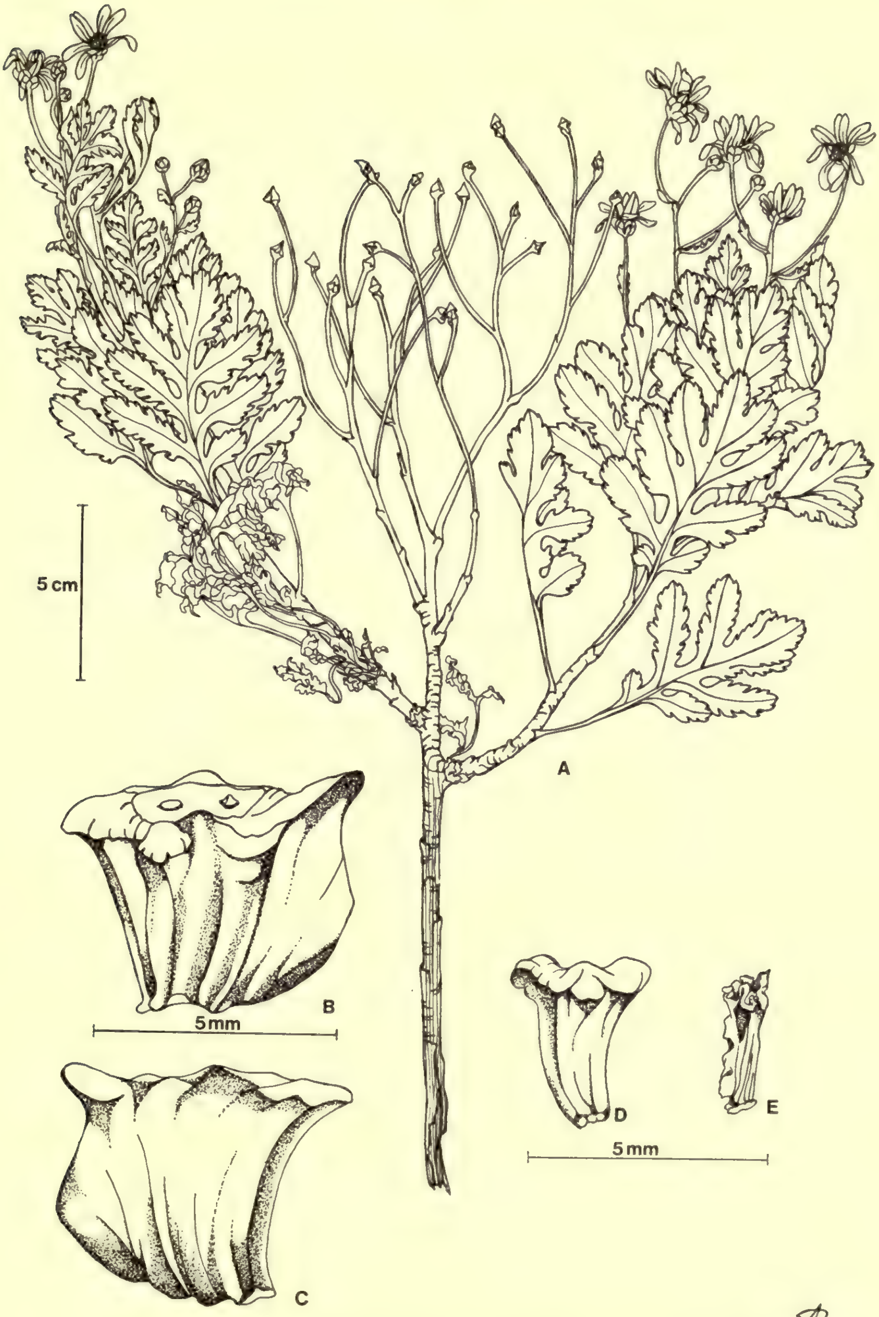

FIG. 21. *Argyranthemum broussonetii* subsp. *gomerensis* C. J. Humphries: A, whole plant; B, ventral view, C, dorsal view of ray cypsela; D, lateral view of disc cypsela of outer series; E, lateral view of disc cypsela of inner series.

Caules 70–80 cm, leviter procumbens vel ascendens. *Folia* 3–10 × 0·5–6 cm. *Involucrum* 13–16 (–19) mm diametro. *Radiorum cypselae* 4–5 mm longae. Plantae endemicae ad Gomeram.

Stems 70–80 cm, slightly procumbent to ascending. *Leaves* 3–10 × 0·5–6 cm. *Involucre* 13–16 (–19) mm diameter. *Ray cypselas* 4–5 mm. Endemic to Gomera.

La Gomera: inter Las Rosas et Agulo, 6 Apr. 1971, *Bramwell & Humphries 3355* (BM ; RNG, holotypus). Degollada de San Sebastian, 9 Apr. 1845, *Bourgeau 247* (BM ; C ; FI ; G ; P ; W ; Z). Riscos de Agulo, 400 m, Apr. 1905, *Pitard* (P).

Found as scattered populations on steep slopes of La Gomera between Las Rosas and Agulo on the north-west coast. A single locality in the Degollada de San Sebastian on south-facing slopes is also recorded (Fig. 20). The habitat is open places in *Laurus azorica* forest and *Adenocarpus foliolosus* scrub. The basal rocks consist of Pliocene basalts covered by more recent phonolytes.

Choisy cited *Chrysanthemum broussonetii* Balbis as the basionym of his *Pyrethrum broussonetii* ; whether this was meant to distinguish Balbis's plant from Persoon's cannot now be determined. De Candolle treated *Chrysanthemum broussonetii* Pers. as a synonym of *C. grandiflorum* var. *subnudum* whilst treating *C. broussonetii* Balbis as a separate species, but gave no reason for doing so. Schultz Bipontinus founded his *Ismelia broussonetii* on *Chrysanthemum broussonetii* Balbis, non Pers., i.e. on *Pyrethrum broussonetii* Choisy, and under *Stigmatotheca lacera* Schultz Bip. had as a synonym 'Chrysanthemum broussonetii. *Pers., Syn., Vol. 2, pag.* 461 (non Balb.), ex specimine in h. paris culto et in herb. Desf! asservato'. Persoon's type, however, is the species under consideration, and Choisy's, De Candolle's and Schultz's accounts of *Chrysanthemum* or *Ismelia broussonetii* also are based on it. One can only assume that the confusion arose because the name became attached in the Paris garden to another species of *Argyranthemum* and it was thought that Persoon's description was based on this. Broussonet sent seeds to Europe of a number of different species of *Argyranthemum*, so this is by no means improbable.

16. ***Argyranthemum hierrense*** C. J. Humphries, sp. nov. (Text-fig. 2O, 3m, n, 22, 23.)

Ismelia coronopifolia sensu Pitard & Proust, Îles Canar., Fl. Archipel : 232 (1908) quoad specim. a Ferro, non Schultz Bip.

Chrysanthemum coronopifolium sensu Burchard in Biblthca bot. 98 : 201 (1929) pro parte, quoad specim. a Ferro, non Masferer. – Ceballos & Ortuño, Veg. Fl. For. Canar. Occid. : 441 (1951) pro parte, quoad specim. a Hierro.

Ab *A. coronopifolium* habitu elatior, inflorescentia multarum capitularum, capitulis parvis, foliis bipinnatifidis, petiolis lanceolatis et cypselis radiorum junctis differt.

Caules 50–80 cm, ascendentes, ramosi per tota planta, glabri. *Folia* 3–9 × 0·6–6 cm, ovata usque deltiodea, bipinnatisecta vel raro tripinnatisecta, glabra, plane petiolata, lobi primarii 2–12, 3–35 × 4–13 mm, oppositi vel suboppositi, lobi secundarii 3–12 × 3–4 mm acuti. *Inflorescentia* corymbosa, 6–50 capitulis, pedunculi 8–10 cm, bracteae foliiformae vel lineo-lanceolatae. *Capitula* subtilia et parva, *involucrum* 5–11 (–16) mm diametro, bracteae series 3 formantes, bracteae extimae triangulares, scariosae, costis carnosis, bracteae intimae obovatae,

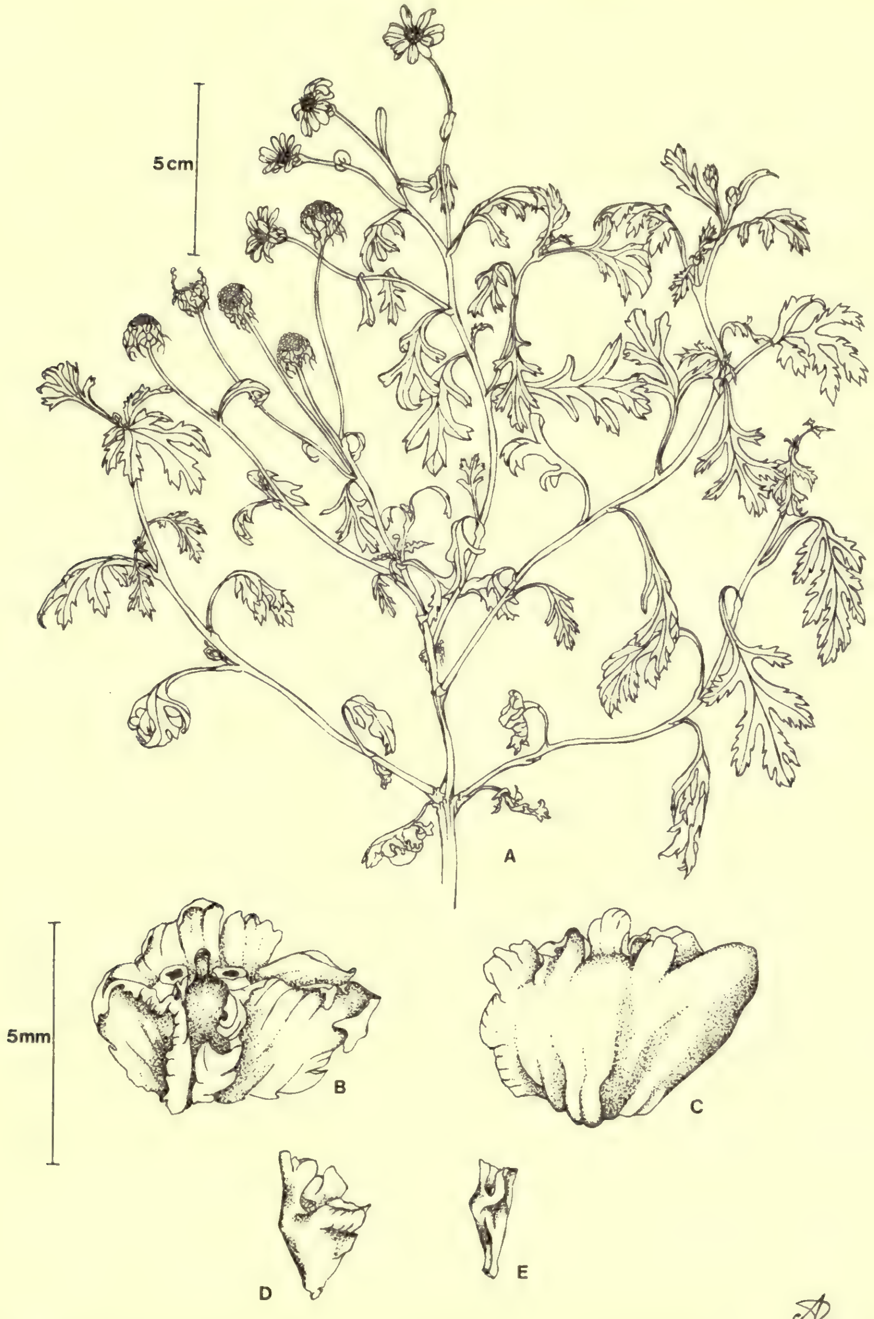

FIG. 22. *Argyranthemum hierrense* C. J. Humphries : A, whole plant ; B, ventral view, C, dorsal view of ray cypsela ; D, lateral view of disc cypsela of outer series ; E, lateral view of disc cypsela of inner series.

scariosae, ad apicem expansae hyalinae. *Radiorum flosculi* 8–17 × *c.* 3·5 mm plus minusve spathulati, albi vel cremei, *discorum flosculi* 2·5–3 mm, lobis corollae flavis et tubis ochroleucis vel albis. *Radiorum cypselae* 3·5–6 × 1·8–9 mm, obconicae, trigonae, arcuatae, 2–4-alatae, dua usque ad quinque saepe coalescentes, pappus coroniformis, dimidiatus vel plus minusve absens ad marginem dorsalem ; *discorum cypselae* 2·5–4 × 1–2·8 mm, obconicae, a latere compressae, in series externas arcuatae, pappus coroniformis, dimidiatus vel absens ad marginem dorsalem seriei extimarum. *Florescentia* Mars usque ad September.

Stems 50–80 cm, ascending, branched throughout the plant, glabrous. *Leaves* 3–9 × 0·6–6 cm, ovate to slightly deltoid, bi-, rarely tri-pinnatisect, glabrous, distinctly petiolate ; primary lobes 2–12, 3–35 × 4–13 mm, opposite to sub-opposite ; secondary lobes 3–12 × 3–4 mm, acute. *Inflorescence* ± corymbose, with 6–50 capitula ; peduncles 8–10 cm ; bracts leaf-like to linear-lanceolate. *Capitula* delicate and small ; *involucre* 5–11 (–16) mm in diameter ; bracts formed of 3 series, outer bracts triangular, scarious with a fleshy midrib, inner bracts obovate with an expanded, scarious, hyaline apex. *Ray florets* 8–17 × *c.* 3·5 mm, ± spathulate to obovate, obtuse, seldom divided at the apex, white to creamy yellow ; disc florets 2·5–3 mm, the corolla lobes yellow, the tube pale yellow or whitish. *Ray cypselas* 3·5–6 × 1·8–9 mm, obconical, trigonous, arcuate, 2–4-winged, often coalesced into groups of 2–5 ; pappus coroniform, dimidiate on the dorsal edge, or absent ; *disc cypselas* 2·5–4 × 1–2·8 mm, obconical, laterally compressed, arcuate in outer series ; pappus coroniform, dimidiate on the dorsal edge in outer series or absent. *Flowering period:* March to September.

Hierro: Scopuli orarum versus Sabinosam, 150 m, 8 June 1971, *Bramwell & Humphries 3317* (RNG, holotypus ; BM, isotypus). Golfo near Roques de Salmar, 9 Apr. 1971, *Bramwell & Humphries 3340* (RNG). Sabinosa, in montane rocks, *Bourgeau 1402* (B ; C ; FI ; G ; K ; P ; W ; Z). North-west of Sabinosa, 150 m, 8 Apr. 1971, *Bramwell & Humphries 3323* (RNG). Same locality, 100 m, *Burchard 174* (K). Same locality, 50 m, May 1924, *Burchard 388* (G ; S ; Z). Sabinosa, 10–350 m, 25 Sept. 1966, *Lems 5982* (MICH). El Bozo de Sabinosa, Apr. 1905, *Pitard & Proust 191* (G ; L ; P). Riscos de Sabinosa, 400 m, Apr. 1906, *Pitard* (G ; P). Valle de Sabinosa, 29 Mar. 1855, *Perraudière* (P). Same locality, 1 May 1855, *Perraudière* in herb. Schultz Bip. (P). Same locality, 500 m, Mar. 1855, *Perraudière* (P ; S).

A locally common endemic on the north-west-facing slopes of the Ensonada de Golfo between Sabinosa and Roques del Salmar.

At lower altitudes between 10 and 350 m it forms the dominant species of the xerophytic zone and is associated with *Euphorbia balsamifera* and *Kleinia neriifolia* communities ; but it also extends at higher altitudes between 200 and 500 m in more widely dispersed populations, to the lower reaches of the *Laurus azorica* forest and the *Erica arborea* zone. The basal rocks consist of Pliocene basalts and Quaternary phonolytes (Fig. 23).

Coastal populations tend to have the caespitose habit of *A. coronopifolium* with fewer and larger capitula than plants from higher altitudes, and in fact have been considered by Burchard (in herbarium material) to represent a form of it with smaller

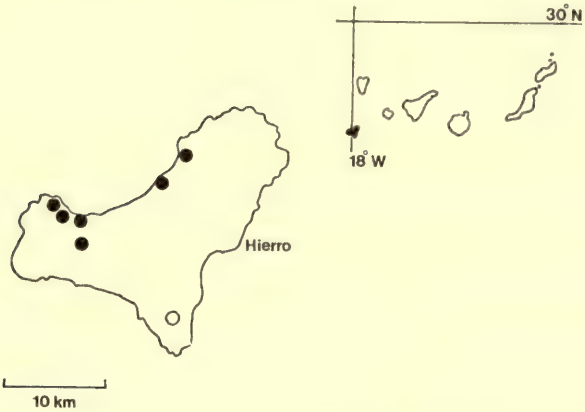

FIG. 23. Distribution of *Argyranthemum hierrense* (●) and *A. sventenii* (○) on Hierro.

flowers and dissected leaves. It differs generally in a number of characters, but notably by its erect habit, the narrowly petiolate, dissected leaves, the proliferous inflorescences, the smaller ligules and involucre, and the coalescent ray cypselas.

17. ***Argyranthemum webbii*** Schultz Bip. in Webb & Berthel., Phyt. Canar. 2 : 269 (1844). (Text-fig. 2P, 3k, 11 ; Pl. 29a.)

Argyranthemum pinnatifidum Webb in Webb & Berthel., tom. cit. : t. 95, quoad fig. 1 (1840), *nom. invalid.*

Chrysanthemum webbii (Schultz Bip.) Masferer in An. Soc. esp. Hist. nat. 10 : 207 (1881), reimpr. ut Rec. Bot. Tenerife : 131 (1881).

Stems 40–85 cm, erect, branched towards the base, or unbranched, glabrous. *Leaves* 4–14 × 2–7 cm, obovate-elliptical in outline, bipinnatifid, narrowly petiolate, glabrous ; primary lobes 4–8, 1–5·2 × 0·2–1·5 cm, opposite to subopposite, dentate ; secondary lobes acuminate. *Inflorescence* corymbose with 2–8 capitula ; peduncles 3–12 cm ; bracts leaf-like to narrowly oblong, dentate. *Involucre* 8–14 mm in diameter ; bracts in 3 series ; outer series triangular, scarious with fleshy midribs ; inner bracts obspathulate or linear-lanceolate, scarious, with an expanded hyaline apex. *Ray florets* 12–22 × 2·5–4 mm, white, the apex emarginate to 3-fid ; *disc florets c.* 3 mm, the corolla lobes yellow, the tube whitish. *Ray cypselas* 5–6·2 × 3·5–8 mm, obconical, ± trigonous, solitary or coalesced into groups of 2 or 3, the wings 2–3, coriaceous, diminutive ; the pappus a marginal coriaceous ridge ; *disc cypselas* 3–4 × 1·9–3·2 mm, obconical, laterally compressed to ± terete, 1-winged ; pappus ± coroniform or a marginal coriaceous ridge. *Flowering period:* February to June.

La Palma: In convalle del Rio, in herb. Schultz Bip. (P, holotypus ; RNG, phototypus). Same locality, in herb. Webb (FI, isotypus). Los Tilos, 6 Sept. 1969, *Bramwell 1831* (RNG). Same locality, Bco. del Agua, 14 Apr. 1971, *Bramwell & Humphries 3409* (BM ; RNG).

A rare endemic of La Palma, confined to the north-east slopes of the Caldera de la Palma, above Los Tilos in the Barranco del Agua and above Santa Cruz de la Palma in the Barranco del Rio. It is intimately associated with the laurel forest, between 500 and 900 m. The basal rocks consist almost entirely of Miocene phonolytic lavas (Fig. 11).

18. ***Argyranthemum haemotomma*** (Lowe) Lowe, Man. Fl. Madeira : 463 (1868). (Text-fig. 2Q, 17.)

Chrysanthemum haemotomma Lowe in Hooker's J. Bot. 8 : 296 (1856).
C. barretti Costa in Broteria 23 : 123 (1927).

Stems 60–120 cm, somewhat decumbent to ascending, ± branched from the base, glabrous. *Leaves* 2–7 × 1–3 cm, obovate or ovate, pinnatisect to bipinnatisect, petiolate, glabrous, rigid, fleshy with sphacelate margins; primary lobes 2–6, 0·5–2·5 × 0·2–0·8 cm opposite; secondary lobes dentate, alternate, acute. *Inflorescence* monocephalic or with 3–4 capitula; peduncles up to 20 cm; bracts 1–2, leaf-like to oblong lanceolate, or absent. *Involucre* 15–20 mm in diameter; bracts in 3 series, outer bracts triangular, scarious, with fleshy midribs, sometimes slightly carinate towards the base, inner bracts obovate with an expanded, scarious, hyaline apex. *Ray florets* 12–15 × *c.* 3·5 mm, pink, rose or white, the apex obtuse to emarginate; *disc florets* 2–3 mm, the corolla-lobes deep purple, the tubes pale pink or whitish. *Ray cypselas* 4–6 × 3–6 mm, unequally triquetrous, arcuate, 3–4-winged; lateral wings carinate, diminutive, the ventral wings 1–2, wider than the laterals, with sinuate margins; pappus coroniform, dimidiate or reduced completely on the dorsal edge, often pointing forwards on the ventral edge; *disc cypselas* 3–5 × 2–3 mm, obconical, laterally compressed to ± quadrangular, 2-winged in the outer series, to 1-winged near the centre of the disc; pappus coroniform, dimidiate, or absent on dorsal margin, sometimes absent completely in the centre series of the disc. *Flowering period:* June to July.

Madeira: Deserta Grande, 2 June 1849, *Lowe* (BM, lectotypus). Same locality, 18 June 1855, *Lowe 832* (BM; G). Madeira 1856, *Mason 334* (CGE). Bugio, 400 m, 1865–66, *Mandon* (G). Same locality, *Lowe* in herb. Moriz (BM). Porto Moniz, 1926, *Costa* (MADM).

An extremely rare species from Deserta Grande and Bugio, Las Desertas islands, south-east of Madeira, occurring as an obligate chasmophyte of wet coastal cliffs between 50 and 450 m. The basal rocks consist of basalts and trachytes of probable Miocene origin. Tentative records from the north-west of Madeira near Porto Moniz are also indicated, but this is based on two very mature specimens only, completely lacking floral parts.

Section 3. ***STIGMATOTHECA*** (Schultz Bip.) C. J. Humphries

ARGYRANTHEMUM sect. STIGMATOTHECA (Schultz Bip.) C. J. Humphries, comb. et stat. nov.

Stigmatotheca Schultz Bip. in Webb & Berthel., Phyt. Canar., 2 : 245, 255 (1844), excl. sect. *Otopappus*.

Plants glabrous. *Leaves* ± entire to pinnatilobed, shortly petiolate to ± sessile. *Ray florets* white. *Ray cypselas* turbinate, trigonous, irregularly ribbed, with 1–3 vestigial wings or wingless; pappus absent, or with a crispate margin; *disc cypselas* obconical, terete to quadrangular, rarely compressed, with 1–2 vestigial wings or wingless; pappus marginal, crispate.

19. **Argyranthemum pinnatifidum** (L. f.) Lowe, Man. Fl. Madeira: 460 (1868). (Text-fig. 30, p, q, r, 24.)

Chrysanthemum pinnatifidum L. f., Suppl. Pl.: 377 (1781). – DC., Prodr. 6: 66 (1838), excl. syn. D. Don.
Matricaria pinnatifida (L. f.) Desrouss. in Lam., Encycl. Meth., Bot. 3: 729 (1792), excl. [var.] *β*.
Pyrethrum pinnatifidum (L. f.) Choisy in Buch., Phys. Beschreib. Canar. Ins.: 149 (1825), non *P. pinnatifidum* Willd. (1803).
Pyrethrum grandiflorum sensu Holl in Flora, Jena 13: 382 (1830), non Willd.
Stigmatotheca pinnatifida (L. f.) Schultz Bip. in Webb & Berthel., Phyt. Canar. 2: 255 (1844).
Chrysanthemum lacerum Buch. ex Lowe, op. cit.: 461 (1868), *nom. synon.*

Stems 30–150 cm, decumbent or ascending, with several stems of equal length to give a candelabra-like habit, glabrous, leafy on upper parts only. *Leaves* 4–20 × 0·5–7·5 cm, obovate or oblong-lanceolate, gradually cuneate at the base, ± entire to pinnatilobed, shortly petiolate to sessile, glabrous, crowded at the base of the peduncles with short internodes, and readily caducous below; lobes 3–9, 1–6 × 0·1–1·5 cm, subopposite, dentate, the teeth obtuse to acuminate. *Inflorescence* corymbose, with 2–30 capitula, peduncles stout, up to 30 cm; bracts leaf-like to spathulate-oblong, serrate or sub-entire. *Involucre* 6–15 mm in diameter; bracts in 3 series, the outer ones triangular, with scarious margins and fleshy midribs, the inner ones scarious with a hyaline, expanded, laciniate apex. *Ray florets* 10–20 × 3–6 mm, white, 1–3-fid at apex; *disc florets* 3–4 mm, the corolla lobes yellow, the tube white, hyaline. *Ray cypselas* 3–4 × 3–4 mm, ± obconical, unequally trigonous, arcuate, the wings occasionally 1–3, diminutive, but usually absent; pappus absent or present as a 2–4-toothed coriaceous ridge; *disc cypselas* 2–3 × 1·5–2 mm, obconical, laterally compressed to quadrangular, irregularly ribbed, wingless; pappus a coriaceous ridge or sometimes ± coroniform. *Flowering period:* April to July.

Two subspecies are recognized:

a. subsp. ***pinnatifidum*** (Text-fig. 2R 1.)

Argyranthemum pinnatifidum [var.] *α flaccida* Lowe, Man. Fl. Madeira: 461 (1868) *nom. illeg.*

Stems 50–150 cm. *Leaves* 7–20 × 2·5–5 cm, pinnatilobed, the lobes usually serrate. *Inflorescence* with (2–) 10–30 capitula.

Madeira: Masson, in herb. L. f. 1332.14 apud herb. Smith (LINN, holotypus). Between Seixal and Porto Moniz, 10–25 m, 1 May 1966, *Lems 7632* (MICH). Rabacal, 1000 m, 14 Apr. 1966, *Lems 7444* (MICH). Saõ Vicente, 650 m, 28 Aug.

1954, *Moore* (BM). Pico de Arrieiro, 1500 m, 24 July 1968, *Hansen* (C). Same locality, 24 July 1968, *Kaae* (C). Same locality, 7 May 1952, *Een 116* (S). Ribeira Frio, 1 May 1952, *Een* (S). Same locality, 4 May 1828, *Gay* (K). Same locality, 800 m, *Lems 7543* (MICH). Same locality, *Neer 1853* (S). Same locality, 2 Aug. 1901, *Vahl* (C). Camacha, 15 July 1846, *Lowe 225* (BM). Sera de San Roque, Poco de Neve, Malhada Velha, 1000–1300 m, July 1865, *Mandon 318* (BM ; C ; G ; K ; S). Funchal, Ribeira do Santa Lizia, 1100 m, 2 July 1900, *Bornmüller 818 b* (G). Camara dos Lobos, Aug. 1853, *Welwitsch* (BM). Cabo Girao, 14 Apr. 1966, *Lems* (MICH). Ribeira do Joao Fernandes, 30 June 1952, *Persson* (S). Same locality, 1832, *Lowe* (G-DC). Same locality, 25 Apr. 1827, *Lowe* (K). Same locality, 1828, *Webb* (G-DC).

Azores: San Miguel, Furnao, May 1838, *Holhort 99* (G ; W).

A common plant of Madeira in the central mountains around Curral das Freiras, the principal ravines on the north side of the island, the lower valleys above Funchal on the south coast and Sao Vicente on the north coast (Fig. 24). Introduced at Furnao in the Azores. It is usually found amongst rocks and open clearings of wet ravines and sea cliffs in most parts of the island between 5 and 1500 m.

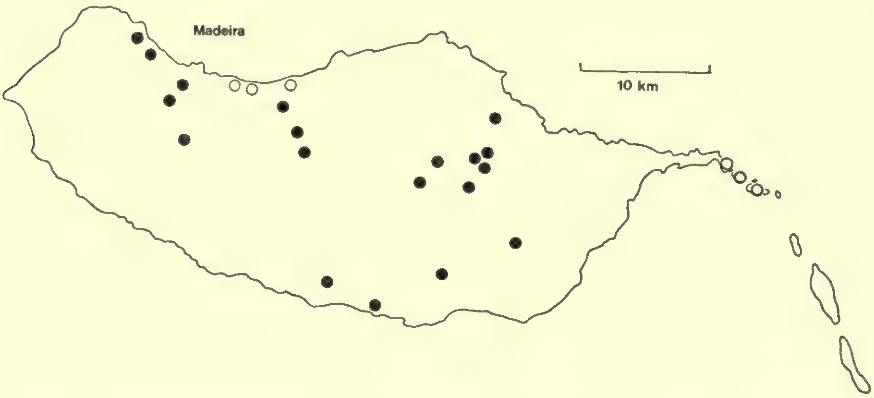

FIG. 24. Distribution of *Argyranthemum pinnatifidum* subsp. *pinnatifidum* (●) and subsp. *succulentum* (○) on Madeira.

b. subsp. ***succulentum*** (Lowe) C. J. Humphries, stat. nov. (Text-fig. 2R 2.)

Argyranthemum pinnatifidum var. *succulentum* Lowe, Man. Fl. Madeira : 462 (1868).
Chrysanthemum mandonianum Cosson in Bull. Soc. bot. Fr. 15 : 100 (1868), *nom. nud.*

Stems 30–45 cm. *Leaves* 4–8 × 0·5–2 cm, fleshy, ± entire with serrate margins. *Inflorescence* with 1–2 (–5) capitula.

Madeira: Punta do San Lorenzo, 6 Mar. 1861, *Lowe 225* (BM ; K, holotypus). Between Seixal and Saõ Vicente, 6 Apr. 1846, *Lowe 936* (BM ; G ; K). Pindo do Saco, 13 Mar. 1860, *Lowe* (BM). Ilheos dos Embarcadores, May 1865, *Mandon 314* (BM ; C ; G ; K ; P ; S ; W). July 1862, *Clarke* (K).

A coastal ecotype of *A. pinnatifidum*, with a very reduced habit and small fleshy leaves, found between Seixal and Saõ Vicente on the central north coast, and

Ponta do Saõ Lourenço on the eastern tip of Madeira. It is also known from the Ilheos dos Embarcardores.

Webb and Bethelot's illustration to which they attached the name *Argyranthemum pinnatifidum* (Phyt. Canar. 2 : t. 95 (1840)) depicts three different plants belonging to separate species, *A. webbii, A. broussonetii* and *A. dissectum.* It would seem that Webb and Berthelot regarded the plants from the Canary Islands with broad bipinnatifid leaves as all belonging to the same species as the Madeiran plants originally described as *Chrysanthemum pinnatifidum* by the younger Linnaeus. As is pointed out above (p. 178), none of the names on Webb and Berthelot's plates were validly published.

Section 4. ***MONOPTERA*** (Schultz Bip.) C. J. Humphries

ARGYRANTHEMUM sect. MONOPTERA (Schultz Bip.) C. J. Humphries, comb. et stat. nov.

Monoptera Schultz Bip. in Webb & Berthel., Phyt. Canar. 2 : 244, 253 (1844).

Plants glabrous. *Leaves* bipinnatisect, distinctly petiolate. *Ray florets* white. *Ray cypselas* clavate to turbinate, arcuate, wingless, usually coalesced into groups of 2–8 ; pappus corniculate when present ; *disc cypselas* obconical, terete, usually wingless ; pappus corniculate when present ; outer series often coalesced with ray cypselas.

20. ***Argyranthemum filifolium*** (Schultz Bip.) C. J. Humphries, comb. nov. (Text-fig. 2S, 3s, t, u, v, 16.)

Monoptera filifolia Schultz Bip. in Webb & Berthel., Phyt. Canar. 2 : 253 (1844). – Pitard & Proust, Îles Canar., Fl. Archipel : 231 (1908).

Chrysanthemum filifolium (Schultz Bip.) Christ in Bot. Jb. 9 : 168 (1887). – Burchard in Biblthca bot. 98 : 201 (1929).

Stems up to 80 cm, ascending, branched towards the base, filiform, glabrous. *Leaves* 1–11 × 2–7, pinnatisect to bipinnatisect, glabrous, with clusters of 2–4 smaller leaves in the axils ; rachis and leaf-lobes filiform, 1–4 mm wide ; primary lobes 1–8, 0·5–6 cm long. *Inflorescence* corymbose ; peduncles 3–25 cm. *Involucre* 6–12 mm in diameter ; bracts in 3 series ; those of outer series triangular with a narrow scarious margin and fleshy midrib ; inner bracts obovate, scarious, with an expanded hyaline apex. *Ray florets* 6–12 × 1·5–2·5 mm, filiform, white, the apex entire or emarginate ; *disc florets c.* 3 mm, the corolla lobes yellow, the tubes hyaline, white. *Ray cypselas* 3–4 × 3·2–6 (–10) mm, arcuate, trigonous, rarely solitary, coalesced in pairs and sometimes in groups of 3–8, the wings 2–4, very small, coriaceous, with irregular margins, or absent ; pappus irregularly cornate, or very rarely a marginal coriaceous ridge ; *disc cypselas* 2–4 × (1·6–) 2–3 mm, obconical-turbinate, usually terete to slightly compressed, coalesced to ray cypselas in outer series, wings usually absent or sometimes 1 ; pappus usually absent but sometimes a corniculate, marginal ridge. *Flowering period:* February to May.

Gran Canaria: J. Despreaux in herb. Webb 198 (FI, holotypus). Between Maspalomas and Tirajana, 9 May 1894, *Murray* (BM ; G ; K). Maspalomas, May 1918, *Burchard 285* (Z). Arguiniguin, 1856, *Bolle* (FI ; W). Same locality, 250 m, 20 Mar. 1969, *Bramwell* (RNG). Same locality, 100 m, 21 Mar. 1971, *Bramwell & Humphries 3060* (BM ; RNG). Same locality, 150 m, 8 Feb. 1969, *Kunkel 12674* (BM). 6 km north-west of Arguiniguin, 2 Nov. 1965, *Lems 6255* (MICH). Puerto de Mogan, 100 m, 21 Mar. 1971, *Bramwell & Humphries 3069* (RNG). 8 km north of Mogan, 21 Mar. 1969, *Bramwell & Humphries 3081* (RNG). Same locality, 11 May 1894, *Murray* (BM ; C ; RHS).

Common along the south coast of Gran Canaria around San Agustin, Maspalomas, Arguiniguin and Puerto de Mogan. Small populations also occur at higher altitudes along the Barranco de Mogan (Fig. 16).

It occurs in the xerophytic vegetation dominated by *Euphorbia obtusifolia* between 50 and 300 m on basal rocks consisting of Miocene phonolytes.

21. **Argyranthemum escarrei** (Svent.) C. J. Humphries comb. nov. (Text-fig. 2T, 16.)

Chrysanthemum escarrei Svent. in Boln. Inst. nac. Invest. agron., Madr. 13 : 69 (1953).

Stems 30–50 cm, erect, branched towards the base, glabrous. *Leaves* 1–8 × 0·5–5 cm, bipinnatisect, petiolate, glabrous ; primary lobes 4–10, 2·5–4·2 × 0·2–0·6 mm, subopposite, linear to linear-lanceolate, acuminate ; secondary lobes linear-lanceolate or dentate. *Inflorescence* corymbose, lax, with 2–8 capitula ; peduncles 2–16 cm ; bracts pinnatisect to linear-lanceolate. *Involucre* 8–14 mm in diameter ; outer bracts triangular, scarious, with a fleshy midrib ; the inner bracts laciniate, hyaline at the apex, linear-oblong, scarious. *Ray florets* 10–14 × 4–6·5 mm, white, the apex obtuse to 3-fid ; *disc florets* 3–5 mm, the corolla lobes yellow, the tubes white. *Ray cypselas* 3·5–4·8 × 2·2–5 mm, obconical, arcuate, trigonous, rarely solitary, usually coalesced in pairs or groups of 3–5, wings 1–2, small, coriaceous or absent ; pappus irregularly cornate ; *disc cypselas* 3–4·5 × 1·6–2·5 mm, obconical, turbinate, terete or 4-angled to laterally compressed, coalesced with ray cypselas in outer series ; pappus irregularly coroniform. *Flowering period:* February to May.

Gran Canaria: Dry rocky cliffs near San Nicolas between 200 and 400 m, 11 Mar. 1950, *Sventenius* (TENE, holotypus). Degollada de Tasartico, 550 m, 21 Mar. 1971, *Bramwell & Humphries 3072* (RNG). Barranco de Tasarte, 600 m, 21 Mar. 1971, *Bramwell & Humphries 3077* (RNG). Tirma, 100 m, coastal cliffs, 28 Mar. 1971, *Bramwell & Humphries 3153* (RNG).

Mountain cliffs of Gran Canaria south of San Nicolas and coastal cliffs north-west of Tirma on the west coast of the island (Fig. 16). The species is found amongst xerophytic *Euphorbia obtusifolia* communities on basal rocks of rhyolite and phonolyte between 200 and 700 m.

Section 5. ***PREAUXIA*** (Schultz Bip.) C. J. Humphries

ARGYRANTHEMUM sect. PREAUXIA (Schultz Bip.) C. J. Humphries, comb. nov.

Preauxia Schultz Bip. in Webb & Berthel., Phyt. Canar. 2 : 244, 250 (1844).
Chrysanthemum sect. *Preauxia* (Schultz Bip.) Christ in Bot. Jb. 9 : 146 (1887).

Plants tomentose to glabrous. *Leaves* bipinnatifid to bipinnatisect, sessile. *Ray florets* white. *Ray cypselas* turbinate, erect, trigonous when single, wingless, and fused together in groups of 2–5 ; pappus a small marginal ridge or absent ; *disc cypselas* obconical, terete, wingless ; pappus absent.

22. **Argyranthemum adauctum** (Link) C. J. Humphries, comb. nov. (Text-fig. 3w, x, y, 25, 26.)

Pyrethrum adauctum Link in Buch, Phys. Beschr. Canar. Ins. : 149, 181 (1825).

Stems 70–90 cm, erect, branched throughout the plant or only from the base, densely tomentose to glabrous. *Leaves* 2–8 (–10) × 0·5–4 (–5) cm, obovate, bi- to tripinnatifid (or pinnatisect), sessile ; primary lobes 4–24, 2–30 × 0·5–15 mm, acute. *Inflorescence* corymbose with 5–20 capitula ; bracts leaf-like to linear-oblong ; peduncles 1–8 (–15) cm. *Involucre* 4–12 mm in diameter ; bracts in 3 series ; triangular to obovate-oblong in outline ; outer bracts fleshy with a narrow scarious border ; inner bracts scarious, usually with an expanded, hyaline apex.

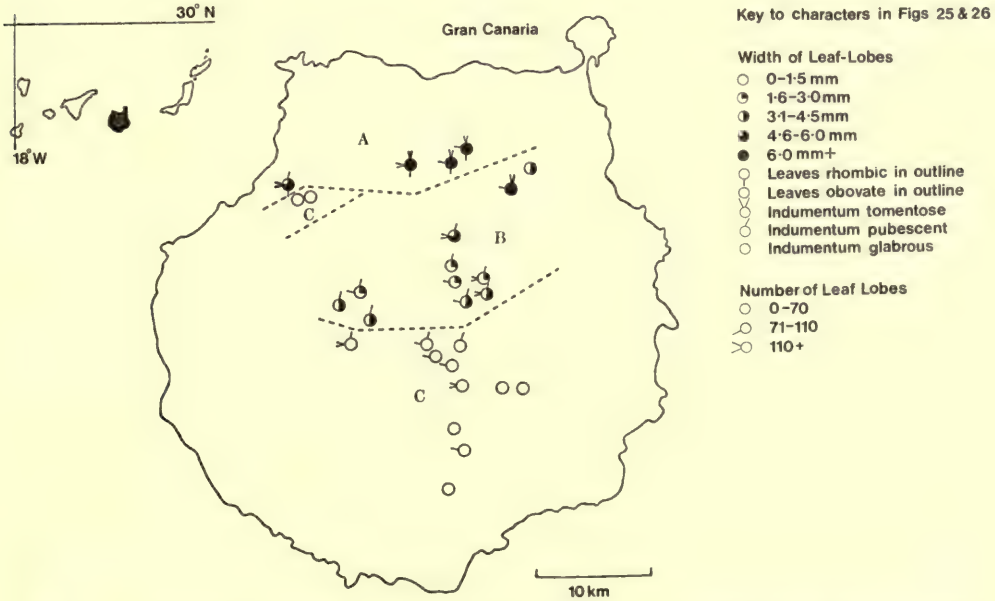
30° N
18°W
Gran Canaria
A
B
C
C
10 km
Key to characters in Figs 25 & 26
Width of Leaf-Lobes
○ 0–1·5 mm
◔ 1·6–3·0 mm
◑ 3·1–4·5 mm
◕ 4·6–6·0 mm
● 6·0 mm+
Leaves rhombic in outline
Leaves obovate in outline
Indumentum tomentose
Indumentum pubescent
○ Indumentum glabrous
Number of Leaf Lobes
○ 0–70
71–110
110+

FIG. 25. Distribution and variation of subspecies of *Argyranthemum adauctum* on Gran Canaria : A, subsp. *jacobaeifolium* ; B, subsp. *canariense* ; C, subsp. *gracile*.

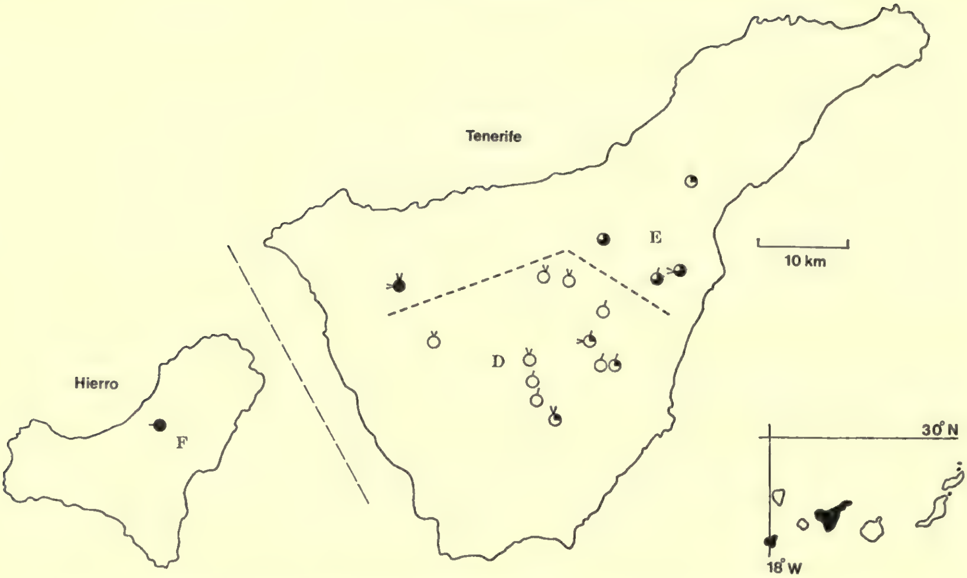

FIG. 26. Distribution and variation of subspecies of *Argyranthemum adauctum* on Tenerife and Hierro : D, subsp. *dugourii* ; E, subsp. *adauctum* ; F. subsp. *erythrocarpon*.

Ray florets 10–15 × 2–3·5 mm, white, the apex 1–3-fid ; *disc florets* 3–4 mm, the corolla lobes yellow, the tubes white. *Ray cypselas* 2·5–4·5 × 1·3–6·5 mm, turbinate, ± trigonous to semi-terete in transverse section, the dorsal surface arcuate, the ventral surface slightly concave or flat, wingless, coalesced together in groups of 2–5 ; pappus absent or present as a narrow marginal ridge with a convex-conical floret abscission scar at the apex ; *disc cypselas* 1·6–2·2 × 0·5–1 mm, obconical, terete, wingless, usually sterile ; pappus nil. *Flowering period:* February to September.

A. adauctum is a relatively widespread species of the western Canary Islands of Gran Canaria, Tenerife and Hierro, in montane scrub, broad-leaved forest and *Pinus canariensis* forest habitats between 350 and 1950 m. Widely dispersed populations are often morphologically distinct and can be grouped into morpho-geographical entities on the basis of vegetative characters. The pictorialized dot maps (Figs 25, 26) indicate the range of distribution and variation in the species with respect to width and number of leaf-lobes, leaf shape and indumentum density. By using these characters, six subspecies can be recognized.

KEY TO SUBSPECIES

Ray cypselas dark brown, the apex becoming black ; inner involucral bracts only slightly expanded at the apex, the margins dark brown, scarious . . . f. *erythrocarpon*

Ray cypselas yellow to chestnut brown ; inner involucral bracts with an expanded, scarious, hyaline apex, the margins light brown to translucent :

  Primary leaf lobes 2–12 mm wide :

    Mature leaves rhombic in outline . . . . c. *jacobaeifolium*

Mature leaves obovate in outline :
  Indumentum subglabrous to glabrous ; basal lobes of leaves usually undivided . . . a. *adauctum*
  Indumentum scabridulous, sometimes tomentose ; basal lobes of leaves divided at least once . . . . b. *canariense*
Primary leaf-lobes up to 2 mm wide :
  Indumentum subglabrous to glabrous . . . . c. *gracile*
  Indumentum scabrid to tomentose . . . . e. *dugourii*

a. subsp. ***adauctum.*** (Text-fig. 2V 4.)

Chrysanthemum grandiflorum [var.] α *adauctum* (Link) DC., Prodr. 6 : 66 (1838).
Preauxia peralderii Schultz Bip. ex Sauer, Cat. Pl. Canar. Ins. : 24 (1880), *nom. nud.* – Pitard & Proust, Îles Canar., Fl. Archipel : 231 (1908), *nom. nud. 'Perraudieri'.*
Chrysanthemum perralderii Christ in Bot. Jb. 9 : 168 (1887) *nom. nud.*
Chrysanthemum anethifolium sensu Burchard in Biblthca bot. 98 : 200 (1929), quoad specim. a Cumbre de Bolico ; non Buch.

Stems 80–120 cm, ascending, branched throughout, subglabrous to glabrous. *Leaves* 4–9 × 2–4 cm, bipinnatifid to bipinnatisect, subglabrous to glabrous ; primary lobes 4–14, opposite to subopposite, dentate, acuminate. *Inner involucral bracts* expanded at the apex. *Ray cypselas* 2·5–4·4 mm ; *disc cypselas* 1·5–2·2 mm, light brown to chestnut in colour.

Tenerife: Moro de Gaitero, 1700 m, 14 Apr. 1969, *Bramwell 1316* (RNG, neotypus). Los Raices, Monte de Esperanza, 2 Apr. 1971, *Bramwell & Humphries 3190* (BM ; RNG). Mirador Ortuño, 2 Apr. 1971, *Bramwell & Humphries 3186* (BM ; RNG). Ladera de S. Ursula, *Laurus* wood, 800 m, *Larsen 1315* (C). Aguamansa, Los Organos, 1200 m, 3 May 1933, *Asplund 1070* (S). Same locality, 1400 m, 8 May 1969, *Bramwell 1482* (RNG). Same locality, 1000–1200 m, 28 Jan. 1933, *Lems 6850, 6893, 6902, 7175* (MICH). Guimar, Bco. del Rio, 700 m, 1933, *Asplund 939* (G ; S). Bco. del Agua, May 1855, *Bourgeau 1387* (C ; FI ; G ; K ; P ; W ; Z). Same locality, 1000 m, 27 Feb. 1855 and 11 Oct. 1855, *Perraudière* (P). Bco. de Valle, 23 May 1879, *Hillebrand* in herb. Christ (Z). La Orotava, 400 m, 27 Sept. 1965, *Lems 6384* (MICH). Cumbre de Bolico, by streams in laurel forest, 1100 m, May 1923, *Burchard 123* (G ; S ; Z). *Broussonet* (BM).

An endemic locally abundant as isolated populations growing along the central Pinar range of Tenerife from Los Raices on the Bosque de la Esperanza to the cliffs at Ladera de Guimar. A single collection is known from the Cumbre de Bolico above the Teno promontory (Fig. 26).

It is usually found growing between 400 and 900 m in *Pinus canariensis* forest, but several collections have been made from *Laurus azorica* forest at lower altitudes. It is also found on rare occasions in the leguminous scrub surrounding the pine forests on the north-west-facing slopes. The basal rocks consist of various types of volcanic lava from the Miocene and later periods.

No particular specimens are indicated in Link's protologue for *Pyrethrum adauctum* which can be traced to the original basic collections of the L. von Buch herbarium at Berlin. As with Bolle's specimens it is likely that all of Link's and indeed Choisy's 'types' for new taxa of Macaronesian Chrysantheminae were destroyed in the great fire of 1943. Link does, however, give the 'locus classicus' as 'Realexo (Realejo) 3300 ft [1000 m]', a locality on the north-facing slopes of Tenerife. This locality must be near the 'Moro de Gaitero' on the Pinar range and in the absence of any possible authentic material I propose to designate a specimen collected by D. Bramwell as the neotype: 'Moro de Gaitero, 1700 m., 14 April 1969, no. *1316*'. The specimen is conserved at RNG.

The habit is characteristic for this subspecies. The plants are very diffuse, with straggling, divaricate branches to form large sub-shrubs with relatively few capitula. It is similar to subsp. *canariense* but differs in the larger, glabrous leaves.

Transitions to subsp. *dugourii* are found above the Ladera de Guimar as the pine forests are replaced by leguminous sub-alpine scrub and the habitats become much more exposed and arid.

b. subsp. ***canariense*** (Schultz Bip.) C. J. Humphries, comb. et stat. nov. (Text-fig. 2V 1.)

Preauxia canariensis Schultz Bip. ex Webb & Berthel., Phyt. Canar. 2 : 252 (1844), excl. forma *gracilis*.

Chrysanthemum canariense (Schultz Bip.) Christ in Bot. Jb. 9 : 146 (1887), excl. var. *tenuisectum*.

Preauxia jacobaeifolia sensu Pitard & Proust, Îles Canar., Fl. Archipel : 231 (1908), non Schultz Bip.

Chrysanthemum canariense var. *jacobaeifolium* Bornm. ex Burchard in Biblthca bot. 98 : 201 (1929) pro parte, non *Preauxia jacobaeifolia* Schultz Bip.

Stems up to 60 cm, ascending, usually branched throughout the plant, pubescent to scabridulous. *Leaves* 1·5–9 × 0·6–4 cm, bipinnatifid to bipinnatisect, pubescent to tomentose; primary lobes 4–20, 2–25 × 2–12 mm, opposite or almost so; secondary lobes 2–6, 1–9 × 3 mm, opposite to alternate, tomentose to pubescent, acute. *Inner involucral bracts* expanded at the apex. *Ray cypselas* 2·5–4·2 mm; *disc cypselas* 1·6–2 mm, light brown to chestnut in colour.

Gran Canaria: in summis Canariae montibus la Cumbre propre montem Saucillo, *Despreaux* in herb. Schultz Bip. (P, holotypus). Bco. Guiniguada, 400 m, amongst rocks, 27 Mar. 1901, *Bornmüller 2461* (G; L; Z). Monte Lentiscal, 450 m, 20 Mar. 1966, *Kunkel 8857* (BM; G). Same locality, *Lowe* (BM; K). San Mateo, 1700 m, 20 May 1900, *Bornmüller 811* (G; P; V; Z). Same locality, 1100 m, pine forest, 15 Feb. 1905, *Pitard 192* (FI; G; L; Z). Same locality, 18 May 1894, *Murray* (BM; RHS). 2 km south of San Mateo, 650 m, 17 Mar. 1971, *Bramwell & Humphries 3008* (RNG). Lagunetas, 24 May 1897, *Gelert* (C). Rincon de Tenteniguada, 600 m, 19 Mar. 1971, *Bramwell & Humphries 3009* (RNG). Same locality, 900–1000 m, Apr. 1924, *Burchard 246* (G; S; Z). Same locality, 1200–1500 m, 30 Oct. 1965, *Lems 6201* (MICH). Cueva Corcho, 9 km south of Valleseco, 700 m, 17 Mar. 1971, *Bramwell & Humphries 3005* (RNG). Saucillo, 28 Apr. 1855, *Bourgeau* (L). Same locality, 2 May 1894, *Murray* (G). Summit of the Cumbre, Apr. 1839, *Despreaux* in herb. Webb 21 (FI). Cruz de Tejeda, 27 Mar. 1969, *Bramwell 1082* (RNG). Artenara, 17 Feb. 1966, *Hulten* (S). Tirajana, Paso de la Plata, Apr. 1846, *Bourgeau 536* (BM; FI; G; K; P; W; Z). June 1912, *Pitard* in herb. Alleizette (L). Lomo Mangrera, 1350 m, 17 Mar. 1967, *Kunkel 10692* (G). 1860, *Despreaux 72* (G). *Christian Smith* (C).

A common plant on the northern slopes of Gran Canaria, extending from Monte Lentiscal in the north-eastern part of the island to Cruz de Tejeda in the west central slopes (Fig. 25). Usual habitats are *Pinus canariensis* savanna at higher altitudes and xerophytic scrubland dominated by *Cytisus canariensis* and *Euphorbia obtusifolia* on lower slopes; 400–1200 m. The basal rocks consist mainly of Miocene basalts, tufts and pouzzolane.

Populations of subsp. *canariense* in the xerophytic scrub of Paso de la Plata, in central Gran Canaria, intergrade with populations of subsp. *gracile*. The transition from one to the other in respect of the habit, and the tomentose, wide, leaf-lobes to glabrous or glabrescent narrow leaf-lobes is very abrupt and instantly recognizable. The vegetative characters are variable between isolated populations throughout the ranges of the recognized subspecies, but generally fall naturally into the two major groups.

c. subsp. ***gracile*** (Schultz Bip.) C. J. Humphries, comb. et stat. nov. (Text-fig. 2V 2.)

Preauxia canariensis forma *gracilis* Schultz Bip. in Webb & Berthel., Phyt. Canar. 2 : 252 (1844).

Preauxia canariensis sensu Pitard & Proust, Îles Canar., Fl. Archipel : 231 (1908), non Schultz Bip.

Chrysanthemum canariense sensu Burchard in Biblthca bot. 98 : 201 (1908), excl. var. *jacobaeifolium*; non Christ.

Stems 50–60 cm, branched from base, subglabrous to glabrous. *Leaves* 0·5–5 × 0·2–3 cm, bipinnatisect, usually glabrous; primary lobes 4–18, opposite to alternate, 0·2–1·8 × *c.* 0·2 cm; secondary lobes 2–12, 0·1–1·8 × 0·1–0·2 cm, subopposite to alternate. *Bracts* and *cypselas* as in subsp. *canariense*.

Gran Canaria: in altibus montibus, *Despreaux* in herb. Schultz Bip. (P, holotypus). Near Tejeda, eastern slopes of Roque Ventaige, 22 Mar. 1966, *Hulten* (S). Los Ardennes de la Mina, 1800 m, May 1914, *Burchard 396* (K; W). Pasa de la Plata, 2 km north of Paso de la Plata, 20 Mar. 1971, *Bramwell & Humphries 3039* (RNG). Same locality, 3 km north, 20 Mar. 1971, *Bramwell & Humphries 3034* (RNG). Artenara, Mna. de Brezo, 1200 m, 28 Mar. 1969, *Bramwell 1121* (RNG). Caldera de Tirajana, below Roque Nublo, 1400 m, 27 Feb. 1969, *Bramwell 1027* (RNG). Same locality, 1000 m, 19 Apr. 1936, *Brookes 116* (BM). San Bartolomé, 3 km north, 780–800 m, 19 Mar. 1971, *Bramwell & Humphries 3014* (RNG). Same locality, 800 m, 18 May 1957, *Larsen* (C). Same locality, 950 m, 16 Feb. 1905, *Pitard 193* (G; L; P; Z). Santa Lucia de Tirajana, 2 km north, on cliffs, *Lems 6230* (MICH). Same locality, 1 km south, 19 Mar. 1971, *Bramwell & Humphries 3013* (RNG). Bco. de Tirajana, *Kunkel 12442* (BM). Temisas, 6 km west, 900 m, 19 Mar. 1971, *Bramwell & Humphries 3010* (RNG). Hoya de la Vieja, 1854, *Bolle* (Z). Bco. de Fataga, 200 m, 30 Aug. 1969, *Bramwell 1184* (RNG). Below Fataga, 200 m, 21 Mar. 1971, *Bramwell & Humphries 3046* (RNG). Near Maspalomas, 9 May 1894, *Murray* (BM; RHS). Pinos de Tamadaba, 25 Mar. 1971, *Bramwell &*

Humphries 3110 (RNG). Above Mogan, *Lowe* (BM). Same locality, 1250 m, 10 May 1967, *Kunkel 11056* (G) June 1839, *Despreaux* in herb. Webb 12 (FI).

A locally common subspecies from the central south-east and southern slopes of Gran Canaria from Artenara and Paso de la Plata, particularly along the barrancos of Tirajana and Fataga. Two distinctive populations have also been collected from the high pine forests at Pinar de Tamadaba (Fig. 25). It is usually found in *Euphorbia obtusifolia* and *Cytisus proliferus* scrub on central and southern slopes but also in open *Pinus canariensis* savannah in the central mountains; 400–1400 m. The basal rocks consist mainly of Pliocene and more recent phonolytes and trachytes.

d. subsp. ***jacobaeifolium*** (Schultz Bip.) C. J. Humphries, comb. nov. (Text-fig. 2U; Pl. 28.)

Argyranthemum jacobaeifolium Webb in Webb & Berthel., Phyt. Canar. 2 : t. 90 (1839), *nom. invalid.*

Preauxia jacobaeifolia Schultz Bip. in Webb & Berthel., tom. cit. : 251 (1844).

Chrysanthemum jacobaeifolium (Schultz Bip.) Christ in Bot. Jb. 9 : 168 (1887).

Preauxia canariensis subsp. *jacobaeifolium* (Schultz Bip.) Bornm. in Bot. Jb. 33 : 484 (1903), *nom. provis.*

Chrysanthemum canariense var. *jacobaeifolium* Bornm. ex Burchard in Biblthca Bot. 98 : 201 (1929), excl. descr.

Stems 70–120 cm, ascending, branched throughout the plant, densely tomentose when young, becoming glabrous when mature. *Leaves* 2–14 × 0·5–6·5 cm, rhombic, bipinnatifid, dark green, pubescent to tomentose; primary lobes 8–32, 0·5–3·5 × *c.* 1·5 cm; opposite or almost so; secondary lobes dentate, acute; apex of *inner involucral bracts* expanded, scarious, hyaline. *Ray cypselas* 2·5–4 mm; *disc cypselas* 1·5–2 mm.

Gran Canaria: 1837, *Despreaux 188,* in herb. Webb (FI, holotypus). Pinos de Tamadaba, 1300 m, pine forests, 23 June 1969, *Bramwell 2226* (RNG). Same locality, 1350 m, pine forest cliffs, 25 Mar. 1971, *Bramwell & Humphries 3111* (BM; RNG). Firgas, 13 May 1891, *Murray* (K; RHS; S). Monte Doromas, high rocky regions, 5 May 1855, *Bourgeau 1389* (C; FI; G; K; Z). Casa Doromas, 26 May 1882, *Hillebrand* (Z). Teror, 20 May 1894, *Murray* (K). Bco. de la Vingua, 13 May 1892, *Murray* (K; S). 'S.S. Virginis', 30 Mar. 1846, *Bourgeau 537* (BM; FI; G; K). *Broussonet* (G). 4 May 1894, *Murray* (K). *Lowe* (K). *Webb* (K).

A rare endemic of north and north-west-facing slopes of Gran Canaria at Firgas, San Matheo, Monte Dormas and steep cliffs at Pinar de Tamadaba (Fig. 25). A tall straggling shrub usually found in shaded *Pinus canariensis* forest and rarely in open scrub of rocky, mountain slopes; 450–1400 m.

Schultz Bipontinus (1844a) considered subsp. *jacobaeifolium* to be a distinct species, *Preauxia jacobaeifolia*. On the basis of the diagnosis, 'Planta herbacea, hirta, receptaculo elongato-conico, foliorum pinnatifidorum lobis oblongis, obtusis dentatis', he separated it from *Preauxia canariensis* (*Argyranthemum adauctum* (Link) C. J. Humphries), 'Planta fruticulosa, hirta, receptaculo depresso-conico, foliorum pinnatipartorum lobis linearibus, acutis, subdentatis'. The separation has its shortcomings as all species of *Argyranthemum* are perennial and have convex-conical receptacles. Also, in sect. *Preauxia*, variation follows more or less a continuum throughout its distribution range in habit, foliage, and fruit characters. From Figs 25 and 26, it is possible to see that there is a parallel north–south cline in reduction of indumentum and leaf area from different localities on Gran Canaria and Tenerife and considerable overlap of variation in most characters in similar habitats from Gran Canaria, Tenerife and Hierro. Thus, populations from north Gran Canaria referable to '*jacobaeifolium*' can only effectively be separated from all other populations in section *Preauxia* by their rhombic-shaped leaves. In general facies, subsp. *jacobaeifolium* is more like its Teneriffean and Hierrean counterparts, referable to subsp. *adauctum* and subsp. *erythrocarpon*.

e. subsp. **dugourii** (Bolle) C. J. Humphries, comb. et stat. nov. (Text-fig. 2V 3.)

Preauxia dugourii Bolle in Bonplandia, Hannover 7 : 297 (1859). – Pitard & Proust, Îles Canar., Fl. Archipel : 231 (1908).
Chrysanthemum dugourii (Bolle) Christ in Bot. Jb. 9 : 146 (1887).
Chrysanthemum canariense var. *tenuisectum* Christ, loc. cit. '*tenuisecta*'.

Stems 60–80 cm, branched from the base, scabridulous to tomentose. *Leaves* 2–6 × 0·3–2 cm, bipinnatisect, scabridulous to tomentose ; primary lobes 6–22, 0·5–2 × *c.* 0·2 cm, opposite or almost so ; secondary lobes 2–10, 0·2–0·6 × *c.* 0·15 cm, opposite to alternate, acute. *Bracts* and *cypselas* as in subsp. *canariense*.

Tenerife: Las Cañadas, El Portillo, between El Cabezon and El Portillo, 2000 m, 14 Apr. 1969, *Bramwell 1315* (RNG). El Sombrerito, 2000 m, 30 Apr. 1969, *Bramwell 1411* (RNG). 2000 m, 11 May 1957, *Larsen* (C). Same locality, 1700 m (Cult. No. 83), *Larsen* (C). Same locality, 1882, *Askenasy* in herb. Christ (Z). Fasnea, 17 June 1855, *Perraudière* (P). Peñones, 6 May 1956, *Lems 2611* (MICH). Llano de Ucanca, 2100 m, 22 May 1957, *Larsen* (C). El Retamar, 2300 m, 10 Apr. 1971, *Bramwell & Humphries 3386* (RNG). Vilaflor, 2 km north-west, 10 Apr. 1971, *Bramwell & Humphries* (RNG). Granadilla, 1954, *Wall 554* (S). Tamadaya, near Arico, 1 Mar. 1855, *Bourgeau 1388* (C ; FI ; G ; K ; P ; W). Near Arico, 700 m, 1926, *Burchard 312* (G ; S ; Z). In Pinetis convallis Tamadaya, *Bourgeau 1388* (C ; FI ; G ; K ; P, neotypus ; W). Same locality, 17 July 1855, *Perraudière* (P). Same locality, 1200 m, 18 June 1855, *Perraudière* (P).

The distribution extends from El Portillo in the north-east region of the Cañadas on Tenerife to the south-facing slopes of Barranco de Pasa Jiron, Lomo de Retama and Vilaflor (Fig. 26). It is a dominant plant of the *Pinus canariensis* forests and also occurs in the sub-alpine, *Spartocytisus supranubius* scrub : 800–2100 m. The basal rocks consist entirely of Quaternary phonolytes.

Subsp. *dugourii* is rather variable in foliage and indumentum characters. It resembles and is often confused with *A. tenerifae* in its chamaephytic habit and erect pinnatisect foliage. It differs, however, by the sectional characters, i.e. the epappose and wingless ray and disc cypselas, the sessile leaves and the obspathulate, inner involucral bracts.

Morphologically it is most similar to subsp. *gracile*, but the leaves are usually larger, more dissected and tomentose.

Bolle's specimens on which he based the description of *Preauxia dugourii* (= *A. canariensis* subsp. *dugourii*) were originally deposited at the Berlin (Dahlem) herbarium. However, there is no material there on which Bolle can be assumed to have based his descriptions, and it seems likely that the specimens were in the herbarium fire of 1943, in the bombing of Berlin, which destroyed them. There are no duplicates at C, FI, W, or Z, where more of Bolle's collections and duplicates are kept.

In the absence of suitable material from the 'locus classicus' (Bco. de Pasa Jiron) cited in Bolle's protologue a neotype has been selected from Bourgeau's well-distributed collections. The label reads *'Tenerife:* Arico in Pinetis Convallis Tamadaya, *Bourgeau 1388*'. Conserved at P ; isotypes C, FI, G, K and W.

f. subsp. ***erythrocarpon*** (Svent.) C. J. Humphries, comb. nov. (Text-fig. 2V 5.)

Chrysanthemum dugourii subsp. *erythrocarpon* Svent. in Index Sem. Hort. Acclim. Pl, Arautapensi 1968 : 52 (1968), reimpr. ut Pl. Macarones. nov. v. minus cogn. 1 : 10 (1968).
Chrysanthemum broussonetii sensu Burchard in Biblthca bot. 98 : 231 (1929), pro parte quoad specim. a Ferro ; non Pers.

Stems 80–100 cm, branched throughout the plant, subglabrous. *Leaves* 3–10 × 0·8–4 cm, bipinnatifid, subglabrous, to glabrous ; primary lobes 6–24, 2–25 × *c.* 8 mm, opposite to subopposite, the lower lobes undissected ; secondary lobes dentate, cuspidate. *Inner involucral bracts* slightly expanded at the apex. *Ray cypselas* 3·5–4·5 mm, dark brown to black, becoming succose at maturity ; *disc cypselas* 1·8–2·2 mm.

Hierro: In the northern pine forests above La Frontera, 10 May 1959, *Sventenius* (TENE, holotypus). La Frontera, 850 m, 7 Mar. 1971, *Bramwell & Humphries 3309* (RNG). Cumbre de Golfo, 800 m, 2 May 1855, *Perraudière* (P).

Found only in *Myrica faya* and *Erica arborea* forest between 600 and 850 m on Hierro. Central mountains of north-west-facing slopes above La Frontera (Fig. 26).

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PLATE 28

Photomicrograph of abaxial leaf surface of *Argyranthemum adauctum* subsp. *jacobaeifolium* to show multicellular glandular hairs and elongated trichomes.

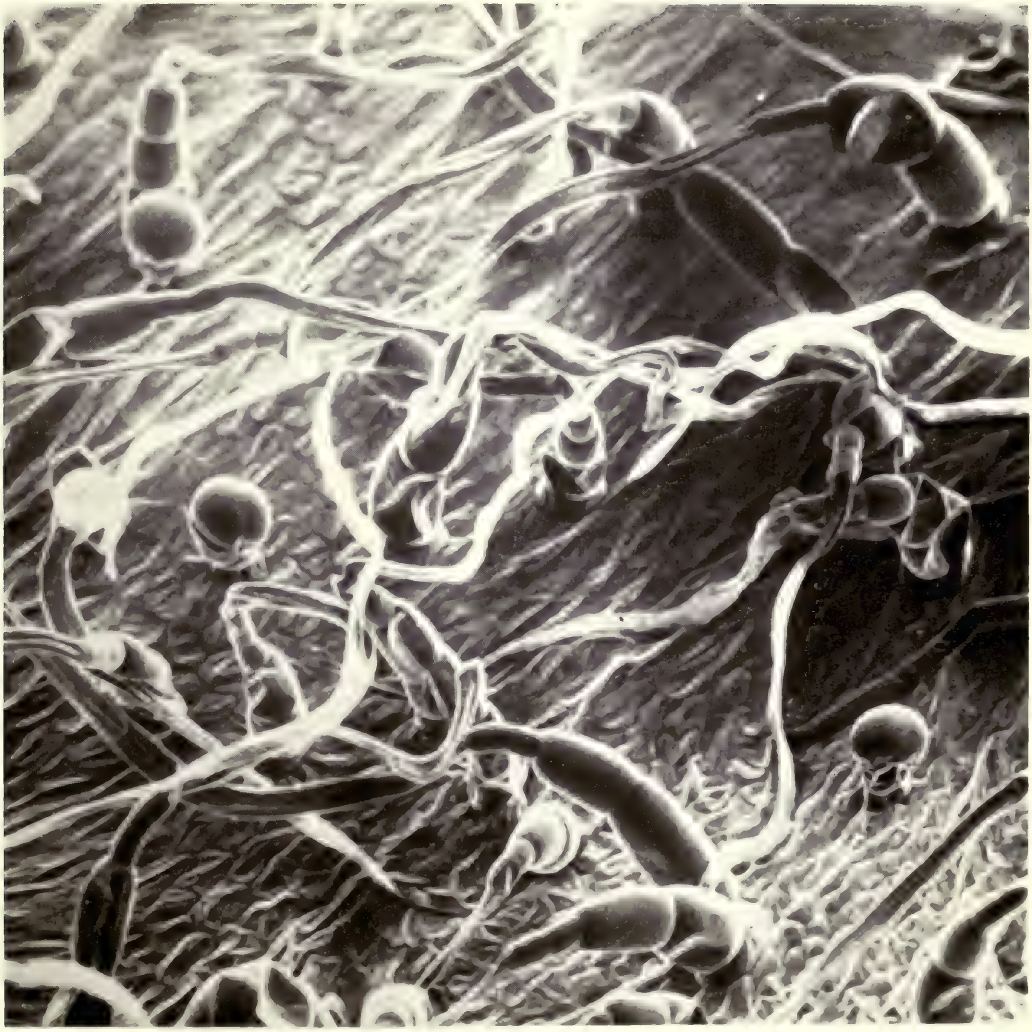
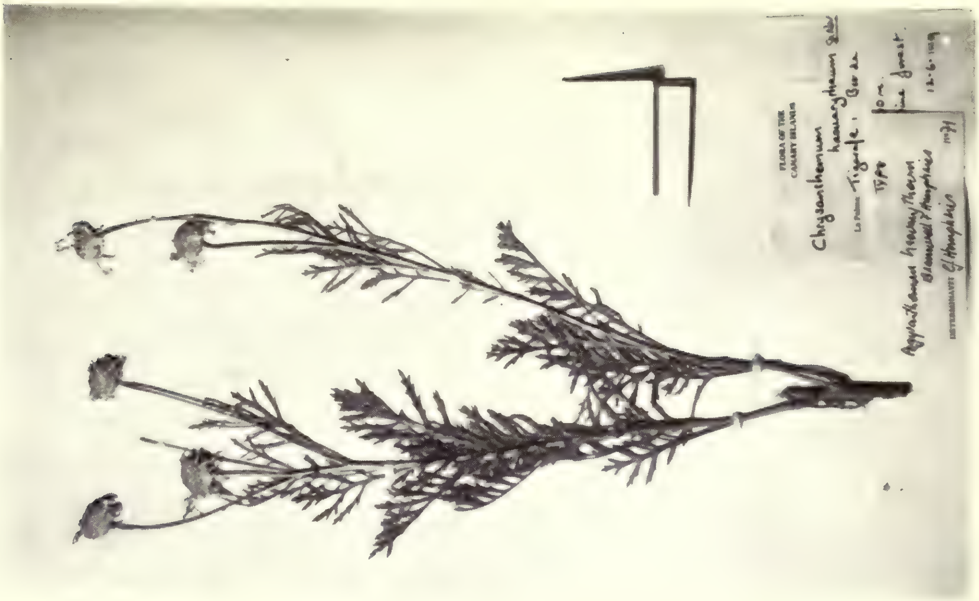


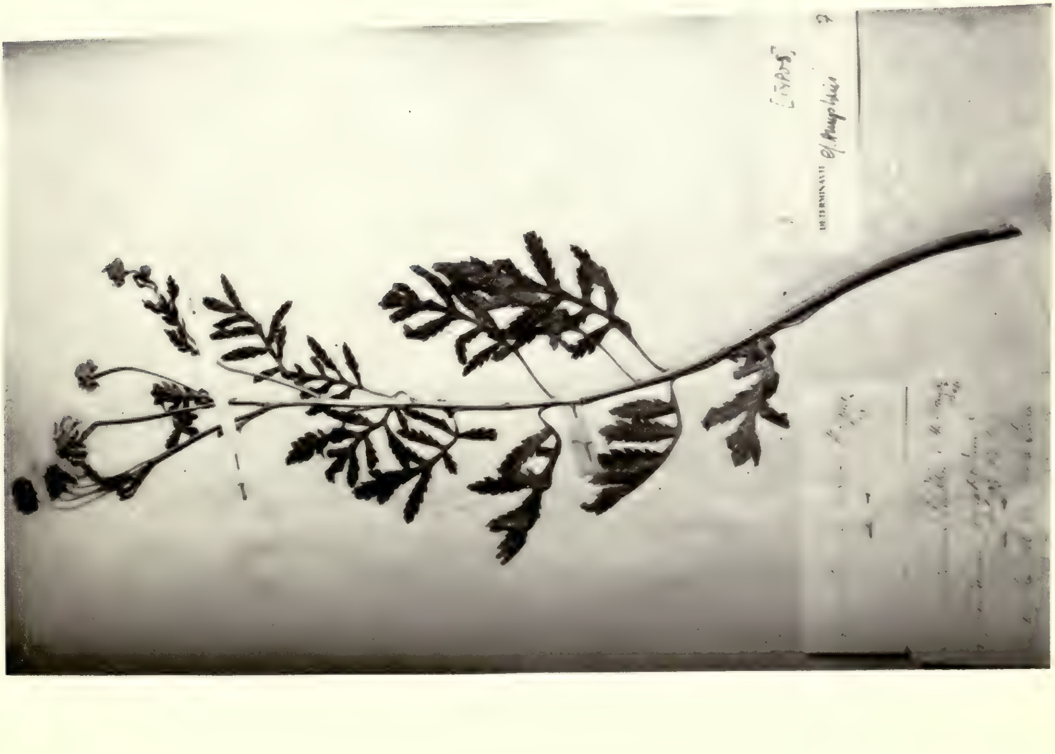
PLATE 29

(a) *Argyranthemum webbii* Schultz Bip. : lectotype from the herbarium of Schultz Bipontinus, Muséum National d'Histoire Naturelle, Paris.

(b) *Argyranthemum haouarytheum* Humphries & Bramwell : holotype, Reading University herbarium.


FLORA OF THE CANARY ISLANDS
TYPE
DETERMINAVIT C. J. Humphries

b


DETERMINAVIT C. J. Humphries
[TYPUS]

a

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FRANK LUDLOW (1885–1972) AND THE LUDLOW-SHERRIFF EXPEDITIONS TO BHUTAN AND SOUTH-EASTERN TIBET OF 1933–1950

W. T. STEARN

RELIQUIAE BOTANICAE HIMALAICAE

FRANK LUDLOW

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
BOTANY Vol. 5 No. 5
LONDON: 1976

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RELIQUIAE BOTANICAE HIMALAICAE

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FRANK LUDLOW

Pp. 241–289 ; 9 Text-figures ; Plates 30–36

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FRANK LUDLOW (1885–1972) AND THE LUDLOW-SHERRIFF EXPEDITIONS TO BHUTAN AND SOUTH-EASTERN TIBET OF 1933–1950

By WILLIAM T. STEARN

SUMMARY

The botanical collections made in Bhutan and south-eastern Tibet between 1933 and 1950 by Frank Ludlow (1885–1972), George Sherriff (1898–1967) and their companions on a series of expeditions amount to over 21,000 gatherings from areas hitherto virtually unknown and constitute a contribution of first importance to knowledge of plants of this area. The first set of their specimens is in the Department of Botany, British Museum (Natural History), with duplicates in other herbaria.

This paper gives a short biography of Ludlow, a list of the Ludlow and Sherriff expeditions with itineraries taken from Ludlow's publications, a gazetteer of their collecting places in south-eastern Tibet and another of places in Bhutan and Sikkim, and a list of Ludlow's publications.

INTRODUCTION

MAINLY for political reasons, which long prevented European entry into the Himalayan region east of Sikkim, i.e. into Bhutan and adjacent south-eastern Tibet, this large area remained botanically almost unknown until 1933 when Frank Ludlow (1885–1972) and George Sherriff (1898–1967) began to reveal its floristic richness by their massive collections. William Griffith had visited Bhutan in 1837 and 1838 and R. E. Cooper in 1914 and 1915 but seemingly William Booth, many of whose collections are attributed to 'Bootan', never got beyond the Balipara Frontier Tract of Assam in 1850, as Ludlow (1972, no. 19) has shown. Thus above all to Ludlow and Sherriff belongs the credit for bridging that gap in our knowledge of the Sino-Himalayan flora between Yunnan and Sikkim. Neither was a botanist by profession. Ludlow's hobbies for many years, while an educationalist and political officer in India, were ornithology and shooting. Sherriff was an army officer who became a keen and successful gardener. From the Royal Horticultural Society, Sherriff in 1953 received its highest honour, the Victoria Medal of Honour, for his services to horticulture by the introduction of plants, but Ludlow, who was justly offered the same honour, refused it, his excessive modesty proof against entreaty. For both, however, plants became their dominating interest during their later years.

As their botanical collections, now in the British Museum (Natural History), amount to over 21,000 gatherings, which have added much to knowledge of plant distribution in the eastern Himalaya and have included many species new to science, it is fitting to summarize their expeditions here.*

---

* Grateful acknowledgement is made to the Editors of *Ibis* and the *Journal of the Royal Horticultural Society* for permission to quote at length from Ludlow's contributions to these journals. A more detailed account of the travels of Ludlow and Sherriff will be found in Harold R. Fletcher, *A Quest of Flowers: the Plant Explorations of Frank Ludlow and George Sherriff told from their Diaries* (xxix + 387 pages; Edinburgh University Press; November 1975), with a long historical introduction by George Taylor, published when the present article was in proof. In addition to portraits of Ludlow and Sherriff and illustrations of plants and scenery, this provides 20 sketch maps which are cited below as: Fletcher, *Quest*, map .... (p. ....).

Few naturalists have been privileged as they were to spend so much time virtually on the roof of the world in virgin territory abounding with beautiful unknown plants; probably none could have made better use of the opportunities thus presented.

Frank Ludlow was born in Chelsea, London, on 10 August 1885 and educated at Wellington School, Somerset, and Sidney Sussex College, Cambridge, where he graduated in 1908 in Natural Sciences. He then joined the staff of the Sind College, Karachi, served during the First World War with the 97th Indian Infantry in Mesopotamia, returned to India and was for three years an Inspector of European Schools at Poona. In 1923 he went to Gyantse in south-eastern Tibet, at the invitation of the Tibetan Government, to set up an educational system and he remained there until 1926, gaining the respect and goodwill of the Tibetans which much aided his later collecting activities in Tibet. This led to his publication of 1927–28 on the 'Birds of the Gyantse neighbourhood' (*Ibis* XII. vols 3–4). In 1927 he moved westward to Srinagar in Kashmir and began to collect birds. While on an expedition to Chinese Turkistan in September 1929 he met George Sherriff at Kashgar and there began the close friendship and the fruitful partnership in activities which lasted until Sherriff's death in 1967. Their first joint plant-collecting expedition was to Central Bhutan in 1933 with F. Williamson, Political Officer in Sikkim, followed in 1934 by one to eastern Bhutan and the Mago district of Tibet.

The success of the 1933 journey led Ludlow and Sherriff to plan for subsequent years a series of expeditions progressing eastward to the great bend of the Tsangpo river, a series which continued, despite interruptions, until 1949. Concerning these expeditions Ludlow wrote in 1968:

> 'In all matters connected with our expeditions Sherriff and I thought alike. There was no disagreement. Our main object was to survey botanically and ornithologically the temperate and alpine regions of Bhutan and South Tibet, and all our efforts were subordinate to this purpose. We realized at the start that the success of our expeditions depended almost entirely on having a happy and contented staff. Our staff was a very mixed one. It consisted of Bhutanese, Sikkimese, Kashmiris and Lepchas, so there was always a danger that on a long journey squabbling and quarrelling would occur. This never happened. Sherriff had the gift of getting the best out of his men. They were well fed, well clothed, well paid, and he made them feel that their work was of great importance, as indeed it was, so they gave of their best. But Sherriff and I were always acutely aware that such success as we achieved was almost entirely due to their loyalty. Without their aid we should not have got very far or done very much.
>
> 'Sherriff was a skilled photographer. When we started collecting in the early thirties photography was a much more tedious process than it is today and a vast amount of time was spent in calculating exposures, changing plates and setting up tripods. Yet, despite these difficulties, Sherriff obtained thousands of pictures, in colour and black and white, of the majority of the plants we met with. These are housed in the British Museum (Natural History), and are available for scientific study.

> 'Transport of living plants by air was in its infancy when we started to collect and Sherriff was one of the first to use this method of transportation. The seeds of some species of plants – petiolarid primulas for instance – become infertile soon after collection and so it becomes necessary to despatch living plants or plants in a dormant state if they are to be introduced. Sherriff sent by air, at no little personal expense, many crates of such plants which on arrival in England were sent to Kew, Wisley, Edinburgh and private gardens.
>
> 'Although transport and supplies in Bhutan and Tibet were cheap, expeditions on the scale we organized were not run without incurring considerable expense. Occasionally we received grants from funds at the disposal of the British Museum (Natural History) and members of the expeditions at times contributed according to their means, but it was Sherriff who defrayed the greater part of the costs. Without his financial help our efforts would have been far more restricted and our collections much more modest.'

In 1938 on an expedition to the Pachakshiri, Takpo and Kongbo districts of Tibet they were joined by Dr G. Taylor (now Sir George), then on the botanical staff of the British Museum (Natural History).

The Second World War interrupted these botanical activities. In 1940 Ludlow became Joint Commissioner in Ladakh, whence he was transferred in the spring of 1942 to take charge of the British Mission in Lhasa, Tibet, an appointment he held for a year ; here he spent his leisure collecting plants and observing birds around the city, the results of the latter being recorded in the *Ibis* **92** : 34–45 (1950) ; the tameness of the birds amazed him. Sherriff replaced him here in 1943 and he returned to Ladakh as Joint Commissioner.

In 1945, in company with Mrs Sherriff and Henry Elliot of the Indian Medical Service, Ludlow and Sherriff made an expedition to the Kongbo and Pome districts of south-eastern Tibet.

In 1947, having reached the age of 60, Ludlow came back to England, returning to India in 1948 and again in 1949 for an expedition to Bhutan. He finally returned to England in 1950. Thereafter most of his life was spent in the Department of Botany, British Museum (Natural History), diligently, quietly and happily studying not only the Ludlow and Sherriff collections but also those of other collectors in the Himalayan region. The intricate genus *Corydalis*, which he knew so well in the mountains, became his major interest and is the subject of the posthumous paper 'New Himalayan and Tibetan species of *Corydalis*' but he also gave critical attention to other groups. In 1956 he published a series of descriptions of new species under the heading 'Novitates Himalaicae'. The posthumous 'Reliquiae botanicae Himalaicae' below give some of the results of his later work.

Unfortunately, Ludlow had a severe accident in 1962, breaking his thigh by a fall on an icy road ; recovery took a long time but he returned to work in the Museum with his customary diligence and enthusiasm. Nevertheless he suffered much from sciatica caused by a couple of intervertebral discs pressing on the sciatic nerve in the lumbar region. His health deteriorated again in the autumn of 1971 ; he became very anaemic. He died at Harefield, Middlesex, on 25 March 1972.

The botanical work of Ludlow's later years is equalled in importance by his ornithological work, as specialists have well recognized. Thus Dr Charles Vaurie dedicated his monumental *Tibet and its Birds* (1972) to Ludlow and remarked that, although helped by many persons and institutions, 'my greatest debt is to Frank Ludlow whose unrivalled experience in southern Tibet and with its birds he has shared with me constantly from the start with the greatest goodwill. My book is dedicated to Ludlow with gratitude and in appreciation for his great contribution to the ornithology of Tibet.' From the ornithological standpoint, Vaurie stated, 'the three expeditions of Ludlow and Sherriff to southeastern Tibet were fruitful beyond all expectations. A large number of species were found in Tibet that had not been suspected to occur north of the main range of the Himalayas, some of them representing families and genera that were new for Tibet. Among them were *Chloropsis hardwickii* (Irenidae) and *Pericrotus ethologus* (Campephagidae), which were new families; three or four flycatchers; more than 20 timaliids, including representatives of nine new genera; and several nonpasserines, chiefly woodpeckers' (Vaurie, *op. cit.*, 75). Ludlow's Fulvetta, *Fulvetta ludlowii* Kinnear, commemorates him.

Ludlow was an extremely likeable colleague whose modesty tended to obscure his great ability and competence, but who always readily made available his extensive knowledge of Himalayan geography, ornithology and botany to any enquirer.

THE LUDLOW AND SHERRIFF EXPEDITIONS

The following summary of the Ludlow and Sherriff expeditions is largely taken from Ludlow's publications; the collecting numbers used on each have been extracted from their field notebooks in the British Museum (Natural History).

1933 (26 April–7 October). Bhutan and Tibet. Nos 1–537.

> 'This was our first expedition. In company with the Williamsons, Sherriff and I travelled along the central highway of Bhutan from Ha to Bumthang. The road is aligned at right angles to parallel ranges given off from the main Himalayan axis and so we were constantly crossing passes and dipping down into adjoining valleys.
>
> 'At Bumthang we met His Highness the Maharaja and then Sherriff and I set off on our own for the Me La on the East Bhutan boundary. This pass, which means in Tibetan the "Pass of Flowers", held a rich flora and we returned to it twice in after years! From the Me La we crossed into the valley of the Kuru Chu, and entered Tibet by the Kang La. Proceeding northwards past the Pomo Tso we struck the Lhasa road at Nangkartse and thence turned west to Gyantse and so back to India. Our collection of five hundred gatherings of plants was small compared with those made on subsequent expeditions. Perhaps the most interesting find was the rediscovery of *Meconopsis superba*, previously known in the wild only from the type-collection of 1884. At the end of this journey Sherriff and I decided on a plan of campaign for the future. In brief this was to work gradually eastwards through Tibet along the main Himalayan range, each succeeding journey overlapping its predecessor, until we reached the great bend

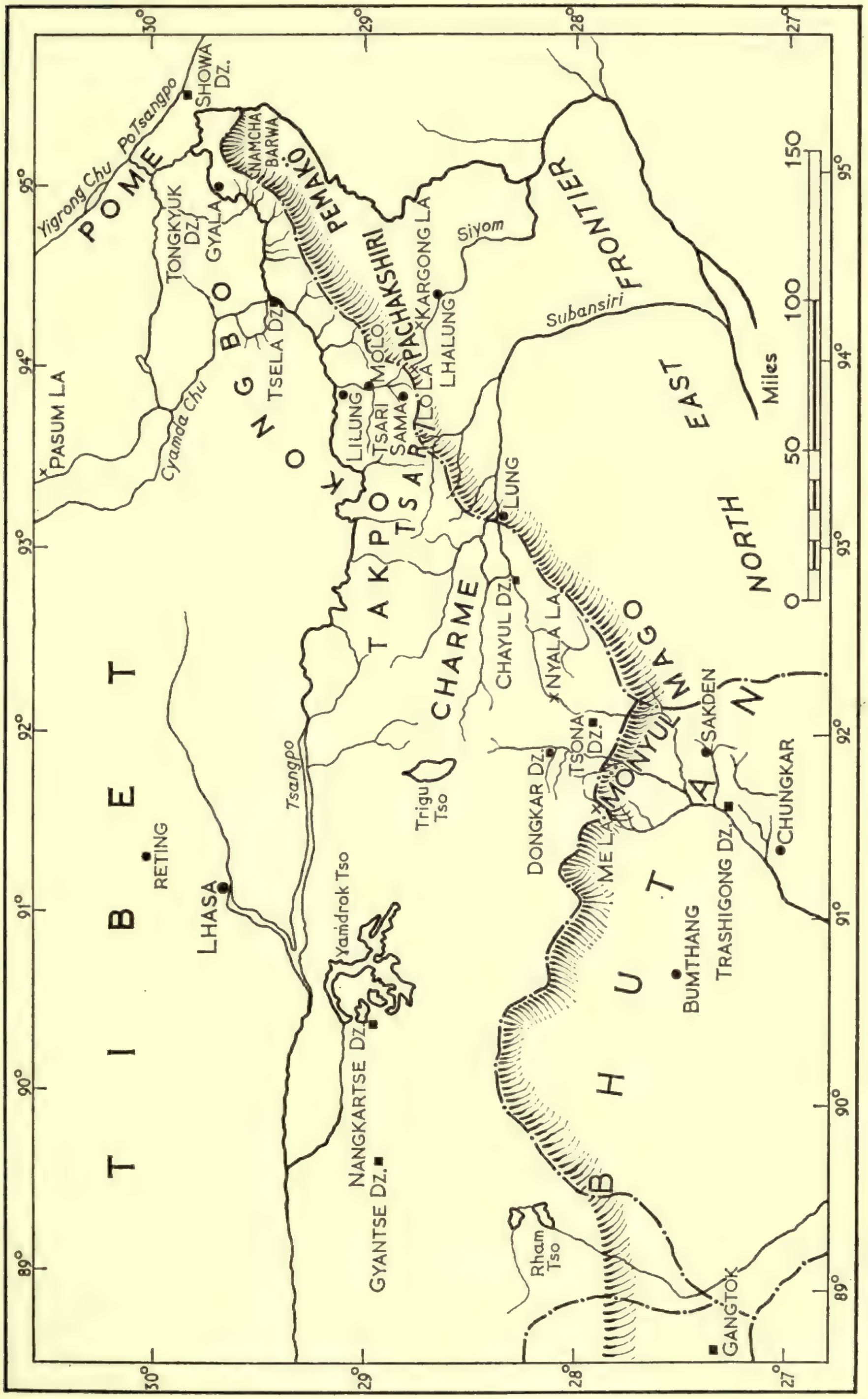
TIBET
LHASA
RETING
PASUM LA
Cyamda Chu
Yigrong Chu
PoTsangpo
POME
SHOWA DZ.
TONGKYUK DZ.
GYALA
NAMCHA BARWA
PEMAKO
KONGBO
TSELA DZ.
LILUNG
MOLO
TSARI
SAMA
LO LA
PACHAKSHIRI
KARGONG LA
LHALUNG
Siyom
Subansiri
FRONTIER
NORTH EAST
TAKPO
TSARI
CHARME
LUNG
CHAYUL DZ.
NYALA LA
Tsangpo
Trigu Tso
Yamdrok Tso
NANGKARTSE DZ.
GYANTSE DZ.
DONGKAR DZ.
TSONA DZ.
MONYUL
MAGO
SAKDEN
ME LA
TRASHIGONG DZ.
CHUNGKAR
BUMTHANG
BHUTAN
Rham Tso
GANGTOK
Miles
0
50
100
150
27°
28°
29°
30°
89°
90°
91°
92°
93°
94°
95°

FIG. 1. Map showing area of the Ludlow and Sherriff expeditions.

of the Tsangpo. Thus progressing gradually eastwards we hoped to obtain valuable information concerning the distribution of plants. In addition to herbarium material the collection of seeds and living plants was also very much in our minds, and also the collection of birds, as the avifauna of the country we proposed to visit was totally unknown.' (Ludlow, 1968.)

Ludlow published a detailed account of this expedition in *Ibis* **79** : 8–13 (1937) with an itinerary giving dates, stages, altitudes and passes crossed (indicated by the Tibetan name *La*) as follows (Fletcher, *Quest*, map 1 (p. 3), map 2 (p. 29)) :

26 April–4 May	Gangtok	6000 ft
5 May	Karponang	9000 ft
6–12 ,,	Changu	12,400 ft
13 ,,	Chumpithang	13,000 ft (Natu La, 14,100 ft)
14–19 ,,	Yatung	9800 ft
20–31 ,,	Sharithang	11,400 ft
1–10 June	Damthang	10,000 ft (Chu La, 14,200 ft, Ha La, 14,000 ft)
11–20 ,,	Ha	9100 ft
21 ,,	Chanana	10,000 ft (Cheli La, 12,500 ft)
22–27 ,,	Paro	7750 ft
28 ,,	Pemitanka	8350 ft (Bela La 11,500 ft)
29 ,,	Tsalimape	7700 ft
30 ,,	Lometsawa	6700 ft (Dokyong La, 10,500 ft)
1–2 July	Wangdi Potrang	4500 ft
3 ,,	Samtegang	7000 ft
4 ,,	Ritang	8200 ft
5 ,,	Chendebi	7500 ft (Pela La, 11,000 ft)
6 ,,	Tsangsa	7500 ft
7–8 ,,	Trongsa	7100 ft
9–10 ,,	Gyetsa	9800 ft (Yuto La, 11,200 ft)
11–17 ,,	Bunthang	9700 ft
18 ,,	Tangnaru	9400 ft
19 ,,	Pimi	9000 ft (Rudo La, 12,600 ft)
20–21 ,,	Khane Lhakhang	8000 ft
22 ,,	Tamachu	5000 ft
23 ,,	Lhüntse	4500 ft
24 ,,	Linji	6500 ft
25–26 ,,	Donga Pemi	10,000 ft
27 ,,	Sana	8400 ft (Donga La, 12,500 ft)
28–30 ,,	Trashiyangsi	5800 ft
31 ,,	Shapang	6500 ft
1 August	Tobrang	7500 ft
2 ,,	Lao	9200 ft
3–10 ,,	Shingbe	12,750 ft (Me La, 14,950 ft)
11 ,,	Lao	9200 ft
12 ,,	Tobrang	7500 ft
13 ,,	Camp (Pang La east)	10,000 ft
14 ,,	Camp (Pang La west)	7500 ft (Pang La, 14,000 ft)
15 ,,	Sawang	6000 ft
16 ,,	Tosumani	10,500 ft
17 ,,	Singhi	12,500 ft
18–28 ,,	Narim Thang	13,900 ft

29 August	Menchumo	14,000 ft (Kang La, 16,300 ft)
30–31 ,,	Hamo	13,500 ft (Pü La, 16,300 ft)
1–2 September	Lhakhang	10,000 ft
3 ,,	Mug	11,500 ft
4 ,,	Singhi Dzong	12,000 ft
5–7 ,,	Towa	12,600 ft
8 ,,	Lhalung	13,100 ft
9 ,,	Mönda	13,500 ft
10 ,,	Pomo Tso	16,200 ft (Monda La, 17,200 ft)
11 ,,	Ling	14,600 ft
12 ,,	Talung	14,700 ft
13 ,,	Nangkartse	14,700 ft
14 ,,	Dzara	15,600 ft
15 ,,	Ralung	14,500 ft (Karo La, 16,600 ft)
16 ,,	Gobshi	13,900 ft
17–24 ,,	Gyantse	13,260 ft
25 ,,	Sowgon	13,500 ft
26 ,,	Khangma	13,900 ft
27 ,,	Kala	14,600 ft
28–29 ,,	Dochen	14,700 ft
30 ,,	Tuna	14,750 ft
1 October	Phari	14,300 ft (Tang La, 15,200 ft)
2–7 ,,	Phari–Kalimpong	(Jelap La, 14,390 ft)

1934 (23 June–9 November). Bhutan and Tibet. Nos 538–1116.

'In accordance with the plan outlined above we made preparations to work the Tsona and Mago districts of Tibet, the former lying north and the latter south of the main axis. Our start was disastrous. Owing to delay in the receipt of our passports we reached rail-head at Rangiya on June 17, the very day the monsoon broke and we were forced to spend a week on a tea estate at the foot of the Diwangiri ravine waiting for the floods to subside. Eventually we got away and took the road to Trashigong and Tsona. On the third day at Chungkar (6,000 feet) we had an extraordinary piece of good fortune. On a cliff face just out of reach Sherriff spotted a lovely mauve primula. Standing on a branch of a large shrub, he discovered another primula, a little scrubby thing, growing in a clump of moss. All three plants were new! The mauve primula became *Primula sherriffiae,* the large shrub *Luculia grandifolia* and the little scrubby plant, *Primula ludlowii.* After this we had more bad luck. At a place called Sakden the whole party, except Sherriff and our two Lepchas, were stricken with malaria, and again we were held up for a week. For a time it looked as if the expedition would have to be abandoned, but we had a good supply of quinine and after a while were sufficiently recovered to proceed to Tsona. It was at Sakden, by the by, that Sherriff found a particularly fine form of *Meconopsis grandis,* known to horticulture as "L & S 600". From Tsona, where *Paraquilegia anemonoides* grew in all its delicate loveliness, we went east to Mago and then returned to Tsona and crossed into the Nyam Jang Chu valley to Dongkar and then south again to the Me La and East Bhutan. Six hundred gatherings of plants resulted from this expedition. We were still a little too selective in our choice of plants.' (Ludlow, 1968.)

Ludlow published a detailed account of this expedition in *Ibis* **79** : 13–19 (1937), including the following itinerary (Fletcher, *Quest*, map 3 (p. 42), map 4 (p. 57), map 5 (p. 63)) :

17–21 June	Menoka Tea Estate	
22 ,,	Diwangiri	2500 ft
23 ,,	Satsalor	3050 ft
24 ,,	Chungkar	6400 ft
25 ,,	Khomanagri	4600 ft
26 ,,	Balfai	6800 ft
27–28 ,,	Ronglung	5000 ft (Yönpu La, 8200 ft)
29 ,,	Trashigong	3250 ft
30 ,,	Rungzyung	4000 ft
1 July	Phongmi	5450 ft
2–10 ,,	Sakden	9700 ft
11 ,,	Muktur	8250 ft
12–13 ,,	Tawang	10,200 ft (Nying Sang La, 12,200 ft)
14 ,,	Shao	13,300 ft (Bum La, 15,000 ft)
15–18 ,,	Tsona	14,300 ft (Kechen La, 15,600 ft)
19 ,,	Thang	14,500 ft (Nyong Chung La, 15,600 ft)
20 ,,	Gu	15,700 ft (Rala La, 16,700 ft ; Gu La, 16,650 ft)
21 ,,	Zangthang	15,400 ft (Dza La, 17,200 ft)
22 ,,	Lungur	13,500 ft (Tulung La, 17,200 ft)
23–25 ,,	Mago	11,600 ft
26 ,,	Camp (Gorja Chu Valley)	12,500 ft (Chera La, 13,500 ft)
27–28 ,,	Lap	14,200 ft
29 ,,	Camp (Gorjo Chu Valley)	12,500 ft
30 July–7 Aug.	Mago	11,600 ft (Chera La, 13,500 ft)
8–14 August	Mago-Tsona	
15 ,,	Camp	15,500 ft (Gorpo La, 17,750 ft)
16–17 ,,	Dongkar	13,350 ft (Sang La, 17,100 ft)
18–19 ,,	Dhukar	13,600 ft (Cha La, 15,300 ft)
20 ,,	Camp	14,300 ft
21 ,,	Karmu	13,000 ft (Cho La, 16,150 ft)
22–27 ,,	Shingbe	12,750 ft (Me La, 14,950 ft)
28 ,,	Lao	9200 ft
29 Aug.–5 Sept.	Tobrang	7500 ft
6 September	Shapang	6500 ft
7–8 ,,	Trashiyangsi	5800 ft
9 ,,	Camp, Dib La	8000 ft
10–14 ,,	Camp, Dib La	12,000 ft
15–20 ,,	Camp, Dib La	11,500 ft
21–24 ,,	Camp, Dib La	10,000 ft
25–29 ,,	Camp, Dib La	8000 ft
30 Sept.–1 Oct.	Trashiyangsi	5800 ft
2–8 October	Sana	8400 ft
9–10 ,,	Trashiyangsi	5800 ft
11 ,,	Shali	6450 ft
12 ,,	Tsirgom	3100 ft
13–14 ,,	Trashigong	3250 ft
15 ,,	Rungzyung	4000 ft

16 October	Phongmi	5450 ft
17 ,,	Taktoo	7850 ft
18–25 ,,	Sakden	9700 ft
26–28 ,,	Taktoo	7850 ft
29 ,,	Phongmi	5450 ft
30 ,,	Rungzyung	4000 ft
31 ,,	Ronglung	5000 ft
1–3 November	Yönpu La	8200 ft
4–5 ,,	Khomanagri	4600 ft
6–8 ,,	Chungkar	6400 ft
9–10 ,,	Satsalor	3050 ft
11–14 ,,	Diwangiri	2500 ft
15 ,,	Rangiya Railway Station	

1935 (11 July–24 September). Kashmir. Nos 1401–1536.

1936 (14 February–3 May). Bhutan and Tibet. Nos 1117–1400.
(3 May–26 November). Tibet and Bhutan. Nos 1537–2917.

'In 1936, with Dr K. Lumsden, we returned to Tsona and then turned eastwards across a high pass called the Nyala La (17,150 feet) into the valley of the Chayul Chu. This river forms the western branch of the Subansiri and we followed it down to Lung (9,000 feet) where it cuts its way through the main range in a heavily forested gorge. Here we encountered a semi-barbaric tribe of Daphlas. From Lung we crossed into the valleys of the Char Chu and Tsari Chu, both of which held a rich flora, particularly the latter. Tsari is holy ground, a place of pilgrimage where cultivation and even grazing are forbidden. As can be imagined it proved a plant hunter's paradise. Whilst Sherriff remained in Tsari and acquired merit by performing the circuit of the holy mountain called Takpashiri, Lumsden and I went east to Molo and then south over the Lo La into Pachakshiri.

'From a horticultural point of view this 1936 expedition was one of the most rewarding we ever made. Amongst the sixty different species of primula collected fourteen were new and the same may be said of rhododendrons of which thirteen were new. In addition, Sherriff discovered the beautiful pink *Meconopsis sherriffii*. The flowering season over, we returned to India by the route followed on our upward journey with nearly two thousand gatherings of pressed plants, two crates of living plants, and innumerable packets of seed.' (Ludlow, 1968.)

Ludlow published an account of this 1936 expedition in *Himalayan Journal* **10**: 1–21 (1938) and in *Ibis* **86**: 45–52 (1944), with the itinerary as follows (Fletcher, *Quest*, map 6 (p. 79), map 7 (p. 87), map 8 (p. 101), map 9 (p. 111), map 10 (p. 121)):

			ft	Lat. ° ′	Long. ° ′
14–21 Feb.	Bhutan	Diwangiri	2100	26 52	91 30
22 Feb.	,,	Satsalor	3000	26 56	91 29
23–25 Feb.	,,	Chungkar	6500	27 03	91 27
26 Feb.	,,	Demri Chu	2500	27 06	91 28
27 Feb.	,,	Jiri Chu	2800	27 08	91 29
28 Feb. to 1 Mar.	,,	Yönpu La	8300	27 13	91 35
2–5 Mar.	,,	Ronglung	5000	27 15	91 34

			ft	Lat. ° ′	Long. ° ′
6 Mar.	Bhutan	Trashigong Dz	4000	27 18	91 34
7 Mar.	,,	Rungzyung	4000	27 20	91 45
8 Mar.	,,	Phongmi	5450	27 20	91 48
9–10 Mar.	,,	? Takhto	7000	27 20	91 52
11–14 Mar.	,,	Sakden	9700	27 21	91 55
15–18 Mar.	,,	Sakden–Trashigong			
19 Mar.	,,	Ghunkarah	3100	27 23	91 35
20 Mar.	,,	Kinney	4900	27 27	91 38
21 Mar.	,,	Changpu	7100	27 29	91 40
22 Mar.	Mönyul	Sanglung	5600	27 30	91 40
23–24 Mar.	,,	Gyipu	7400	27 36	91 43
25–26 Mar.	,,	Shakti	7250	27 38	91 46
27 Mar. to 3 April	,,	Pangchen	7200	27 41	91 48
4 April	,,	Le	8350	27 47	91 50
5–8 April	,,	Lepo	9600	27 53	91 52
9–11 April	,,	Trimo	10500	27 55	91 53
12–15 April	Tsona	Tsona Dz	14300	28 00	92 01
			(Po La, 14900′)		
16 April	,,	Tre	14500	28 05	92 06
			(Doka La, 15500′)		
17 April	,,	Gyisum	15200	28 05	92 10
18 April	Chayul	Loro Tö	14300	28 12	92 15
			(Nyla La, 17150′; lat. 28° 08′, long 92° 13′.)		
19 April	,,	Jora	12700	28 13	92 25
20 April	,,	Tro Shika	12350	28 16	92 34
21–23 April	,,	Chayul Dz	11200	25 18	92 48
24 April	,,	Kap	11400	28 18	92 55
25 April	,,	Trön	10200	28 20	93 01
26–27 April	Abor Country	Natrampa	10000	28 21	93 04
28–30 April	,, ,,	Lung	9200	28 21	93 09
1–6 May	,, ,,	Lung–Chayum Dz.			
7 May	Chayul	Gyandro	13500	28 24	92 49
8–10 May	Charme	Kyimpu	12500	28 25	93 01
			(Le La, 17150′)		
11 May	,,	Charme	10600	28 26	93 05
12–13 May	,,	Sanga Chöling	10700	28 33	93 00
14 May	,,	Zimsatti	14200	28 38	93 03
15 May	Tsari	Chösam	14100	28 44	93 10
			(Cha La, 16600′)		
16–17 May	,,	Senguli	13300	28 43	93 13
18–20 May	,,	Yarap	12400	28 43	93 23
21–22 May	,,	Podzo Sumdo	11000	28 43	93 34
23 May to 1 June	,,	Migyitun	9600	28 40	93 38
2–11 June	,,	Camp (Bimbi La)	12000	28 48	93 28
12–13 June	Takpo	Tsemachi	13700	28 50	93 28
			(Bimbi La, 15700′)		
14 June	,,	Sumbatse	12100	28 52	93 28
15–17 June	,,	Kyimdong Dz	10600	28 59	93 28

			ft	Lat. ° ′	Long. ° ′
18–19 June	Takpo	Taktsa.	13000	28 59	93 32
20 June	Kongbo	Camp	14300	28 58	93 42
			(Lang La, 15800′)		
21 June	,,	Kethong	11500	28 57	93 46
22–24 June	,,	Molo	10300	29 57	93 53
25 June to 1 July	,,	Singo Samba	11400	28 52	93 52
2 July	,,	Camp (Lo La North)	13000		
3 July	Pachakshiri	Camp (Lo La South)	10700		
			(Lo La, 13300′)		
4 July	,,	Chudi	8800	28 43	94 01
5–10 July	,,	Camp (Nyug La)	10000	28 42	94 03
			(Nyug La, 11000′)		
11–15 July	,,	Nyug La–Singo Samba			
16–17 July	Kongbo	Langong	11900	28 51	93 47
18 July	,,	Camp (Pa La)	14600	28 52	94 67
19–20 July	Takpo	Camp (Pa La)	13500		
			(Pa La, 15900′)		
21–22 July	,,	Kyimdong Dzong	10600	28 59	93 28
23 July	,,	Nge	10500	29 01	93 17
24 July	,,	Chote Shu	11100	29 01	93 12
			(Kongbo Nga La, 14570′)		
25 July	,,	Peru	11600	28 51	93 10
26–27 July	,,	Tsobunang	13500	28 46	93 10
28 July	Tsari	Chösam	14100	28 44	93 10
			(Sur La, 15700′; lat. 28° 45′, long. 93° 11′)		
29 July	,,	Chorten Namu	14700	28 44	93 04
30 July to 5 Aug.	Charme	Sanga Chöling	10700	28 41	93 02
			(Cha La, 16600′)		
6 Aug.	,,	Bung	12000	28 34	92 47
7 Aug.	,,	Sho Shika	13000	28 35	92 45
9–10 Aug.	,,	Camp (Traken La)	14500	28 43	92 42
11 Aug.	,,	Karpo	13000		
			(Traken La, 16900′)		
12 Aug.	,,	Camp	15500	28 41	92 57
			(Sokpo La, 16600′)		
13 Aug.	,,	Camp	15000	28 42	92 59
			(Mihrang La, 17000′)		
14 Aug.	Tsari	Chösam	14100	28 44	93 10
15–20 Aug.	Takpo	Tsobunang	13500	28 44	93 10
			(Sur La, 15700′)		
21 Aug.	Tsari	Senguli	13300	28 43	93 13
			(Sur La, 15700′)		
22–24 Aug.	,,	Chikchar	12500	28 42	93 18
25 Aug.	,,	Podzo Sumdo	11000	28 42	93 34
26–29 Aug.	,,	Migyitun	9600	28 40	93 38
30 Aug. to 3 Sept.	,,	Camp (Na La)	12900	28 40	93 39
4 Sept.	,,	Migyitun	9600	28 40	93 38

			ft	Lat. ° ′	Long. ° ′
5–14 Sept.	Tsari	Camp (Bimbi La)	12000	28 48	93 28
15 Sept.	,,	Chikchar	12500	28 42	92 18
16–18 Sept.	,,	Chösam	14100	28 44	93 10
19–20 Sept.	Charme	Zimsatti	14200	28 38	93 03
			(Cha La, 16600′)		
21–26 Sept.	,,	Sanga Chöling	10700	28 33	93 00
27–30 Sept.	,,	Charme	10600	28 26	93 05
1–8 Oct.	,,	Kyimpu	12500	28 25	93 01
9 Oct.	Chayul	Gyandro	13500	28 24	92 49
			(Le La, 17150′; lat. 28° 27′, long. 92° 56′)		
10–11 Oct.	,,	Chayul Dz	11200	28 18	92 48
12 Oct.	,,	Tro Shika	12350	28 16	92 34
13 Oct.	,,	Jora	12700	28 13	92 25
14 Oct.	,,	Loro Tö	14300	28 12	92 15
15 Oct.	Tsona	Gyisum	15200	28 05	92 10
			(Nyala La, 17150′)		
16 Oct.	,,	Tre	14500	28 05	92 06
17–19 Oct.	,,	Tsona Dz	14300	28 00	92 01
			(Doka La, 15500′)		
20 Oct.	,,	Camp, Kechen La	15000		
21 Oct.	,,	Shao	13300	27 45	92 00
			(Kechen La, 15600′)		
22 Oct.	Monyul	Tawang	10200	27 34	91 56
			(Bum La, 15000′; Milakatong La, 14200′)		
23 Oct.	,,	Muktur	8250	27 32	91 58
24–25 Oct.	Bhutan	Sakden	9700	27 21	91 55
			(Nying Sang La, 12200′)		
26 Oct.	,,	Phongmi	5450	27 20	91 48
27 Oct.	,,	Rungzyung	4000	27 20	91 45
28–29 Oct.	,,	Trashigong Dz	4000	27 18	91 34
30 Oct. to 2 Nov.	,,	Yönpu La	8300	27 13	91 35
3–5 Nov.	,,	Khomanagri	4600		
6–10 Nov.	,,	Chungkar	6500	27 03	91 27
11 Nov.	,,	Satsalor	3000	26 56	91 29
12–26 Nov.	,,	Diwangiri	2100	26 52	91 30

1937 (24 April–26 August). Bhutan. Nos 2918–3573.

'Sherriff spent the flowering season in Central Bhutan collecting in the vicinity of a high peak called the Black Mountain, returning with a valuable collection of six hundred gatherings.' (Ludlow, 1968.) Fletcher, *Quest*, map 11 (p. 128).

1937 (November). Tsingpen. Nos 3574–3579.

1938 (20 February–26 November). Tibet, Sikkim and Bhutan. Nos 3580–7289.

'In 1936 we had collected in the upper reaches of the Subansiri. This year we decided to collect within the drainage of the Tsangpo from the vicinity of Molo on the Lilung Chu down to Gyala at the entrance to the gorge. Dr G. Taylor – now Sir George – was our companion on this occasion. Medical reasons prevented him from joining the expedition at Kalimpong in February, so we agreed to meet at Molo in mid-May, and set out for Pachakshiri via the Tsangpo valley. Pachakshiri lies south of the Main Range which had to be crossed by the Lo La – the pass I had used in 1936. The Lo La was deep under snow when we reached it in late April but we scampered over it at night whilst the snow was frozen and in four days reached Lhalung (6,700 feet) on the Siyom. We did well with plants during the twelve days we spent here, but leeches, ticks, and blister flies made life very unpleasant and we were glad to return to Tibet. We reached Molo on May 17, and before we could even pitch camp Taylor arrived from England! Some staff work. A few days were spent in getting re-organized and then we separated. Taylor and I worked the Main Range down to the gorge and Sherriff collected from Tsari Sama to the Kucha La. We met again at Tsela Dzong the end of July, and then I set off alone for the Pasum La leaving Taylor and Sherriff to work the ranges on the lower Gyamda Chu. A fortnight later I received an alarming message from Sherriff to say that Taylor was seriously ill with suspected appendicitis. Happily this was not the case and I returned to find Taylor still weak but on the road to recovery. Eventually he became strong enough to begin the rather arduous return journey to India via Tsari, Tsona and East Bhutan. On this expedition we amassed a vast amount of herbarium material, over four thousand gatherings. With Taylor urging us to be less selective in our methods, we took everything we saw, from lichens to lilies. We collected seed also on a large scale and living plants as well. It is sad to reflect that the outbreak of World War II largely nullified our efforts.' (Ludlow, 1968.)

Ludlow published an account of this expedition in *Himalayan Journal* **12**: 1–16 (1940) and in *Ibis* **86**: 52–60 (1944) with an itinerary as follows (Fletcher, *Quest*, map 12 (p. 156), map 13 (p. 171), map 14 (p. 191), map 15 (p. 214), map 16 (p. 223)). The abbreviation 'Dz' is used here for 'Dzong', meaning fort.

			ft	Lat. ° ′	Long. ° ′
20–24 Feb.	Sikkim	Kalimpong–Kupup			
25 Feb. to 13 Mar.	S. Tibet	Kupup–Gyantse, via Tang La, 15200′, and Jelap La, 14390′			
14–19 Mar.	,,	Gyantse–Kongka Dz, via Karo La, 16800′			
20–25 Mar.	,,	Kongka Dz–Tsetang by coracle down the Tsangpo			
26 Mar.	,,	Rongchakar	12050	29 13	92 03
27–28 Mar.	,,	Lhagyari	13100	29 06	92 12
29 Mar.	Takpo	Lasor	12200	29 05	92 25
			(Pitrang La, 16500′)		
30 Mar.	,,	Lhapso	11650	29 06	92 32

			ft	Lat. ° ′	Long. ° ′
31 Mar.	Takpo	Lenda	11000	29 09	92 42
1 April	,,	Rabdang	10800	29 06	92 50
2–3 April	,,	Tromda	10800	29 05	92 55
4 April	,,	Nang Dz	10700	29 03	93 10
5 April	,,	Nge	10600	29 01	93 17
			(Kongbo Nga La, 14570′; lat. 29° 01′, long. 93° 12′)		
6–10 April	,,	Kyimdong Dz	10600	28 59	93 28
11 April	,,	Taktsa	13000	28 59	93 32
12 April	Kongbo	Camp	13000	28 58	93 42
			(Lang La, 15800′; lat. 28° 58′, long. 93° 42′)		
13 April	,,	Kethong	11500	28 57	93 46
14–20 April	,,	Molo	10300	29 57	93 53
21 April	,,	Camp, Langong Chu	11000	28 51	93 47
22–23 April	,,	Camp, Lo La North	12500	28 50	93 57
24 April	Pachakshiri	Camp, Lo La South	10700		
			(Lo La, 13300′)		
25 April	,,	Chudi	8800	28 43	94 01
26 April	,,	Camp	8000	28 42	94 03
			(Nyug La, 11000′)		
27 April to 8 May	,,	Lhalung	6300	28 42	94 12
			(Kargong La, 8800′; lat. 28° 42′, long. 94° 11′)		
9–17 May	,,	Lhalung–Molo, via Nyug La and Lo La			
18–23 May	Kongbo	Molo	10300	29 37	93 53
24 May	,,	Charko	10000	29 04	93 56
25 May	,,	Lilung	9800	29 07	93 54
26 May	,,	Simbiteng	9900	29 11	93 56
27 May	,,	Yusum	9700	29 11	94 01
28 May	,,	Shoka	9600	29 14	94 09
29 May	,,	Kangka	9600	29 18	94 16
30 May to 4 June	,,	Tse	9600	29 23	94 22
5 June	,,	Chamna	9800	28 26	93 05
6 June	,,	Lusha	9500	29 27	94 35
7 June	,,	Camp	10500		
8–14 June	,,	Camp, Lusha La	12500	29 20	94 35
			(Lusha La, 14600′)		
15–17 June	,,	Lusha	9500	29 27	94 35
18 June	,,	Tamnyen	9500	29 27	94 38
19–23 June	,,	Camp	10800	29 20	94 43
			(Tamnyen La, 14500′)		
24 June	,,	Tamnyen	9500	29 27	94 38
25–26 June	,,	Sang	9600	29 29	94 41
27–30 June	,,	Camp	13500		

			ft	Lat. ° ′	Long. ° ′
1–3 July	Kongbo	Tumbatse	11600 (Sang La, 14500′ approx.)	29 42	94 47
4 July	,,	Camp	13500 (Nyima La, 15200′)	29 38	94 52
5 July	,,	Timpa	9700	29 33	94 52
6–7 July	,,	Pe	10000	29 31	94 54
8 July	,,	Tripe	10000	29 36	94 56
9–10 July	,,	Gyala	9300	29 43	94 56
11–12 July	,,	Gyala–Pe			
13–16 July	,,	Camp	12500 (Doshong La, 13500′)	29 29	94 59
17–19 July	,,	Pe	10000	29 31	94 54
20–23 July	,,	Pe–Gyala			
24–27 July	,,	Gyala–Pe			
28 July	,,	Tamnyen	9500	29 27	94 38
29 July	,,	Chamna	9800	29 25	94 26
30 July to 6 Aug.	,,	Tse	9600	29 23	94 22
7–9 Aug.	,,	Tsela Dz	9700		
10 Aug.	,,	Mape	9800	29 33	94 20
11 Aug.	,,	Chomo Dz	9900	29 38	94 16
12 Aug.	,,	Nyarlu	9900	29 41	94 09
13 Aug.	,,	Dzeng	9900	29 47	93 55
14 Aug.	,,	Tongshong	10000	29 52	93 48
15–16 Aug.	,,	Namse	10100	29 53	93 46
17 Aug.	,,	Nye	10400	29 56	93 47
18 Aug.	,,	Drukla Gompa	11000	30 05	93 45
19 Aug.	,,	Nanda	11300	30 07	93 32
20 Aug.	,,	Pangkar	11800	30 17	93 31
21 Aug.	,,	Camp	12100		
22–23 Aug.	,,	Camp	14000 (Pasum La, 17250′)	30 27	93 22
24 Aug.	,,	Pangkar	11800	30 17	93 31
25 Aug.	,,	Pang	11200		
26 Aug.	,,	Shoga Dz	10600	30 00	93 48
27 Aug.	,,	Drepang	10800	30 00	93 50
28 Aug.	,,	Pasum Tso	10800	30 01	94 01
29 Aug.	,,	Lotu	10800	30 01	94 14
30 Aug.	,,	Camp	13500		
31 Aug.	Pome	Nambu Gompa	13800 (Nambu La, 14970′; lat. 29° 59′, long. 94° 26′)	29 59	94 31
1 Sept.	,,	Camp	11500		
2 Sept.	,,	Ketang	9000	30 00	94 47
3 Sept.	,,	Tongkyuk Dz	8600	29 56	94 50
4 Sept.	,,	Chunyima	10900	29 48	94 45
5 Sept.	Kongbo	Tumbatse	11600	29 42	94 47
6 Sept.	,,	Camp	13000 (Temo La, 14000′)	29 35	94 37

			ft	Lat. ° ′	Long. ° ′
7–15 Sept.	Kongbo	Dzeng	9500	29 29	94 30
16 Sept.	,,	Lusha	9500	29 27	94 35
17–19 Sept.	,,	Camp	12500	29 30	94 35
			(Lisha La, 14600′)		
20–22 Sept.	,,	Lsuha	9500	29 27	94 35
23 Sept.	,,	Chamna	9800	29 25	94 26
24–26 Sept.	,,	Tse	9600	29 23	94 22
27 Sept.	,,	Kangka	9600	29 18	94 16
28 Sept.	,,	Shoka	9600	29 14	94 09
29 Sept.	,,	Miling	9600	29 11	94 05
30 Sept.	,,	Trongsa	9600	29 11	93 58
1–4 Oct.	,,	Lilung	9800	29 07	93 54
5 Oct.	,,	Gacha	10200	29 07	93 41
6 Oct.	,,	Trome	10000	29 10	93 33
7 Oct.	,,	Kamchang	10100	29 06	93 29
8–11 Oct.	Takpo	Kyimdong Dz	10600	28 59	93 28
12 Oct.	,,	Sumbatse	12100	28 52	93 28
13 Oct.	,,	Tsemachi	13700	28 50	93 28
14 Oct.	Tsari	Camp	12000	28 48	93 28
			(Bimbi La, 15700′)		
15 Oct.	,,	Chikchar	12500	28 42	93 18
16 Oct.	,,	Chösam	14100	28 44	93 10
17 Oct.	Charme	Zimsatti	14200	28 38	93 03
			(Cha La, 16600′; lat. 28° 41′, long. 93° 02′)		
18–20 Oct.	,,	Sanga Chöling	10700	28 33	93 00
21 Oct.	,,	Charme	10600	28 26	93 05
22 Oct.	,,	Kyimpu	12500	28 25	93 01
23 Oct.	Chayul	Gyandro	13500	28 24	92 49
			(Le La, 17150′; lat. 28° 27′, long. 92° 56′)		
24 Oct.	,,	Chayul Dz	11200	28 18	92 48
25 Oct.	,,	Yar Shika	12000	28 14	92 40
26 Oct.	,,	Jora	12700	28 13	92 25
27 Oct.	,,	Loro Tö	14300	28 12	92 15
28 Oct.	Tsona Dz	Tre	14500	28 05	92 06
			(Nyala La, 17150′)		
29 Oct.	,,	Tsona Dz	14300	28 00	92 01
			(Doka La, 15500′)		
30–31 Oct.	Mönyul	Trimo	10500	27 55	91 53
			(Pö La, 14900′)		
1 Nov.	,,	Le	8350	27 47	91 50
2 Nov.	,,	Pangchen	7200	27 41	91 48
3 Nov.	,,	Shakti	7250	27 38	91 46
4 Nov.	,,	Kapteng	5600	27 33	91 43
5 Nov.	Bhutan	Changpu	7100	27 29	91 40
6 Nov.	,,	Ghumkarah	3100	27 23	91 35
7–8 Nov.	,,	Trashigong Dz	4000	27 18	91 34
9–26 Nov.	,,	Trashigong Dz–Diwangiri			

1939 (16 June–17 August). Simla Hill States. Nos 7300–7540.
(20 August–24 September). Kashmir. Nos 7560–8577.

1941 (August–September). Assam. Nos 10092–10094.

1942 (16 March). Kashmir. No. 8578.
(30 March–5 October). Sikkim and Tibet (Lhasa). Nos 8579–9103.
(7 August–24 December). Sikkim. Nos 10095–10114 D.
(6–18 October). Sikkim and Tibet. Nos 10000–10091.

1943 (10 March–11 October). Sikkim and Tibet (Lhasa). Nos 9444–9962.
(21 June–27 August). Kashmir. Nos 9104–9385.

1944 (9–13 July). Tibet (Reting). Nos 9963–9999.
(13 July–13 September). Tibet (Lhasa). Nos 11000–11155.
(24–25 October). Mishmi Hills. No. 11156.

1945 (28 April). Tibet. No. 11157.
(30 May). Sikkim. No. 11158.

'The war, of course, destroyed all hopes of further expeditions, at least for as long as it lasted. However, in the spring of 1942 I was sent to Lhasa as Assistant Political Officer in charge of the British Mission and was succeeded in this post by Sherriff with his wife in the spring of 1943. During our stay in Lhasa we collected most of the plants that grew within a radius of 60 miles. There were a number of novelties especially from an area called Reting 60 miles north of Lhasa. One of our more interesting "finds" was the re-discovery of *Meconopsis torquata* first obtained in 1904 by Walton on the Younghusband Mission.' (Ludlow, 1968.)

Ludlow published a note on his stay at Lhasa in 1942–43 in *Ibis* **92**: 34–36 (1950).

1946 (24 May). Kashmir. No. 9402.

1946 (21 October–1947 (4 October). Tibet. Nos 12000–12692, 13000–13390, 13500–15831.

'The war over we set out again for S.E. Tibet, this time with Betty Sherriff and Colonel Henry Elliot of the Indian Medical Service. We decided on winter travel to enable us to reach our collecting grounds in Pome and the great gorge of the Tsango by early spring. Travelling through the familiar Tsangpo valley we reached Tongyuk Dzong in Pome on Xmas day and Trulung (6,000 feet) on the Po Tsangpo early in the New Year. After visits to the lower Yigrong and Showa we returned to Trulung where the Sherriffs descended the Po Tsangpo to its junction with the Tsangpo at Gompo Ne. About this time Sherriff, who never spared himself on any expedition, began to suffer from an overstrained heart, and after consultation with Elliot he decided, very reluctantly, to return to lower altitudes in India. The departure of the Sherriffs rather upset our plans, but Elliot and I agreed that at all costs we *must* explore the Tsangpo gorge, so we set out for Gyala at the entrance, and after four difficult marches, reached Pemakochung, a small flat at the mouth of a glacial valley descending from Namcha Barwa. All around us rhododendrons flowered in great profusion, but there were no paths as the gorge is uninhabited and the only tracks were those of Takin. We had to hack our way through this jungle and did not progress more than 1,000 yards from the flat on which we were camped. Nevertheless in the four days we spent at Pemakochung we obtained twenty-three different species of rhododendrons! Some day someone will spend a flowering season in this great gorge and what a harvest he will reap! After our descent of the gorge Elliot and I separated, he to work valleys in the upper Yigrong whilst I worked the southern slopes of the range north of Shoga Dzong. Our Lepcha plant collector we sent to Showa in Pome, but here he found the inhabitants uncooperative and returned prematurely. This was to prove our last Tibetan expedition though we didn't realize it at the time. In October, Elliot and I began our return journey via the Tsangpo valley, a barren route, botanically uninteresting which we did not wish to take, but which we were compelled to follow.' (Ludlow, 1968.) (Fletcher, *Quest*, map 17 (p. 253), map 18 (p. 273)).

Ludlow published an account of this expedition in *Ibis* **93** : 547–553 (1951), and in volumes 141–143 of the *Gardeners' Chronicle* (1957–58).

1948 (28 February–19 April). India and Sikkim. Nos 15832–15847.

1949 (27 March–23 October). Sikkim and Bhutan. Nos 16000–17572, 18500–21484.

'We had both left India and this was to be our final fling. Strange to relate we planned to separate. Sherriff was attracted by the Mishmi Hills and I by the vision of a summer in the Tsangpo gorge. Both our applications were refused so we turned again to Bhutan, and once more His Highness the Maharaja gave us permission to travel wherever we wished. On this occasion we decided to work the whole of temperate and alpine Bhutan from west to east, and for this purpose we split up into three parties. Dr J. H. Hicks, who had joined us as Medical Officer and Mrs Sherriff went to East Bhutan, Sherriff to Central Bhutan, and I to the western region. Our collection of five thousand gatherings was the largest we ever made, and included the remarkable *Lilium sherriffiae* with tessellated brown and yellow flowers. An unfortunate accident, however, marred this last journey in July. Owing to a loose saddle girth Mrs Sherriff fell from her mule and broke an arm. Hicks was not able to set this and it was thought advisable for her to return to India for an X-ray. On reaching Kalimpong it was found that all was well and further treatment unnecessary. And so we came to the end of our travels.' (Ludlow, 1968.) (Fletcher, *Quest*, map 19 (p. 309), map (p. 329)).

1950. Bhutan. Nos 21486–21599.

Gazetteer of Ludlow and Sherriff Localities. Tibet

Locality	Latitude	Longitude	Locality	Latitude	Longitude
Adju La	29° 52′ N	95° 08′ E	Besang Landup	30° 25′ N	93° 48′ E
			Bimbi La	28° 47′ N	93° 29′ E
Bachumo	30° 05′ N	94° 43′ E	Bira Tso	29° 59′ N	94° 15′ E
Ba La	30° 22′ N	94° 09′ E	Bo	30° 11′ N	93° 30′ E
Barang Shika	28° 55′ N	93° 53′ E	Budi Tsepo La	29° 27′ N	94° 57′ E

Gazetteer of Ludlow and Sherriff Localities. Tibet (*cont.*)

Locality	Latitude	Longitude
Buku	30° 21′ N	93° 34′ E
Bum La	27° 43′ N	91° 55′ E
Bung	28° 34′ N	92° 49′ E
Cha	29° 34′ N	94° 18′ E
Cha La	28° 41′ N	93° 02′ E
Chab	29° 45′ N	94° 11′ E
Chachima	30° 02′ N	94° 15′ E
Chaksam (bridge over Tsangpo near Lhasa)	29° 21′ N	90° 44′ E
Chakzam (bridge over Yigrong Chu)	30° 07′ N	95° 08′ E
Chamna	29° 25′ N	94° 26′ E
Changlung Chago	30° 00′ N	95° 30′ E
Changpu (Bhutan and Mönyul Frontier)	27° 30′ N	91° 40′ E
Charme	28° 26′ N	93° 05′ E
Chayul Dzong	28° 18′ N	92° 48′ E
Chera La	27° 39′ N	92° 15′ E
Chikchar	28° 43′ N	93° 22′ E
Chilung La	28° 22′ N	91° 52′ E
Chiniung La	28° 41′ N	93° 50′ E
Chira	29° 14′ N	91° 28′ E
Chitisha	29° 18′ N	91° 07′ E
Cho La	28° 02′ N	91° 47′ E
Chomo Dzong	29° 38′ N	94° 16′ E
Chongye Dzong	29° 07′ N	91° 44′ E
Chösam	28° 44′ N	93° 10′ E
Chubumbu La	28° 41′ N	93° 48′ E
Chudi Chu (at source of Siyom on Lo La)	28° 49′ N	94° 00′ E
Chukor	29° 27′ N	94° 21′ E
Chumdo	30° 05′ N	95° 43′ E
Chumpithang	27° 25′ N	88° 53′ E
Chunyima	29° 48′ N	94° 49′ E
Chupung La	28° 19′ N	93° 12′ E
Chushal	29° 22′ N	90° 44′ E
Dechen Dzong	30° 00′ N	90° 38′ E
Dem	30° 02′ N	95° 15′ E
Deyang La	29° 22′ N	94° 52′ E
Dochen	28° 09′ N	89° 18′ E
Doka	30° 07′ N	95° 07′ E
Doka La	28° 02′ N	92° 02′ E
Dokar	29° 49′ N	95° 20′ E
Dongkar Dzong	28° 09′ N	91° 55′ E

Locality	Latitude	Longitude
Dore	30° 25′ N	93° 48′ E
Dorjitra	29° 19′ N	91° 09′ E
Doshong (Doshung)	29° 32′ N	94° 51′ E
Doshong La	29° 29′ N	94° 59′ E
Drepung Gompa	29° 40′ N	91° 02′ E
Drichung La	28° 24′ N	93° 00′ E
Drölma La	28° 39′ N	93° 21′ E
Drukla Gompa	30° 05′ N	93° 45′ E
Dyuri	27° 40′ N	92° 13′ E
Dza La	27° 58′ N	92° 12′ E
Dzala	30° 15′ N	94° 02′ E
Dzam	29° 10′ N	92° 33′ E
Dzama	29° 56′ N	95° 07′ E
Dzara	28° 53′ N	90° 15′ E
Dzeng (Gyamda Chu Valley)	29° 47′ N	93° 55′ E
Dzeng (near Tsela Dzong, Tsangpo Valley)	29° 29′ N	94° 30′ E
Egar	30° 25′ N	93° 50′ E
Gacha	29° 07′ N	93° 42′ E
Ganden Gompa	29° 41′ N	91° 27′ E
Gautsa	27° 35′ N	89° 03′ E
Gobshi	28° 50′ N	89° 51′ E
Gompo-ne	29° 50′ N	95° 11′ E
Gorpa La	28° 08′ N	91° 59′ E
Guru Namgye Dzong	29° 02′ N	92° 58′ E
Gyachung La	28° 27′ N	91° 43′ E
Gyadzong	30° 11′ N	95° 05′ E
Gyala	29° 42′ N	94° 56′ E
Gyala Peri	29° 49′ N	94° 58′ E
Gyamda Dzong	30° 01′ N	93° 07′ E
Gyandro	28° 24′ N	92° 49′ E
Gyantse Dzong	28° 53′ N	89° 33′ E
Gyare	29° 58′ N	93° 50′ E
Gyatsa Dzong	29° 10′ N	92° 42′ E
Gyipu	27° 36′ N	91° 43′ E
Gyisum	28° 05′ N	92° 10′ E
Je	30° 02′ N	94° 02′ E
Jora	28° 13′ N	92° 25′ E
Kala (Yigrong Valley)	29° 58′ N	93° 49′ E
Kala (Phari–Gyantse Road)	28° 16′ N	89° 25′ E
Kamchang	29° 05′ N	93° 30′ E

Gazetteer of Ludlow and Sherriff Localities. Tibet (*cont.*)

Locality	Latitude	Longitude
Kangma	28° 33′ N	89° 41′ E
Kap	28° 18′ N	92° 55′ E
Kapteng	27° 33′ N	91° 44′ E
Kargong La	28° 42′ N	94° 11′ E
Karma La	29° 56′ N	95° 07′ E
Karo La	28° 54′ N	90° 11′ E
Karpo	28° 41′ N	92° 51′ E
Karutra Temple	28° 21′ N	93° 11′ E
Kashong La	28° 20′ N	93° 08′ E
Kechen La	27° 55′ N	91° 59′ E
Kethong	28° 57′ N	93° 46′ E
Khamba La	29° 12′ N	90° 32′ E
Khambapadze	29° 13′ N	90° 33′ E
Kongbo-nga-La	29° 01′ N	93° 12′ E
Kongkar (Gangkar) Dzong	29° 16′ N	90° 46′ E
Kucha La	29° 13′ N	94° 33′ E
Kumang	29° 44′ N	94° 58′ E
Kyabden	29° 39′ N	94° 17′ E
Kyikar	29° 37′ N	94° 56′ E
Kyimdong Dzong	28° 59′ N	93° 28′ E
Kyimpu	28° 25′ N	93° 01′ E
Lamdo	29° 20′ N	94° 19′ E
Lang La	28° 58′ N	93° 42′ E
Langong	28° 46′ N	93° 48′ E
Langpe	29° 38′ N	94° 55′ E
Lap	27° 38′ N	92° 23′ E
Lapu	28° 42′ N	93° 22′ E
Lasor	29° 05′ N	92° 25′ E
Layoting	30° 00′ N	94° 55′ E
Le	27° 47′ N	91° 50′ E
Le La	28° 27′ N	92° 56′ E
Lenda	29° 09′ N	92° 47′ E
Lepo	27° 53′ N	91° 52′ E
Lhagyari Dzong	29° 06′ N	92° 12′ E
Lhakang Dzong	28° 04′ N	91° 04′ E
Lhalung (Halung, in Pachakshiri Dist.)	28° 42′ N	94° 12′ E
Lhapsö Dzong	29° 07′ N	92° 32′ E
Lhasa	29° 40′ N	91° 05′ E
Ligding	29° 27′ N	94° 23′ E
Lilung	29° 08′ N	93° 54′ E
Ling	28° 44′ N	90° 34′ E
Ling La	28° 37′ N	90° 33′ E
Lingtsang La	28° 48′ N	93° 41′ E
Lisum	30° 06′ N	94° 30′ E
Lochen	30° 28′ N	93° 38′ E
Lochen La	30° 25′ N	93° 35′ E
Lokmo	30° 01′ N	94° 45′ E
Lo La	28° 58′ N	93° 58′ E
Lolung Leku	29° 12′ N	94° 27′ E
Loro Tö	28° 12′ N	92° 15′ E
Lotu	30° 01′ N	94° 14′ E
Lubong	29° 58′ N	95° 06′ E
Luguthang	27° 32′ N	92° 11′ E
Lung	28° 21′ N	93° 09′ E
Lunang	29° 44′ N	94° 48′ E
Lusha	29° 27′ N	94° 35′ E
Lusha La	29° 18′ N	94° 37′ E
Makandro	29° 54′ N	95° 02′ E
Mera La	29° 30′ N	94° 09′ E
Migyitun	28° 40′ N	93° 34′ E
Mihrang La	28° 42′ N	92° 59′ E
Milakatong La	27° 41′ N	91° 57′ E
Miling	29° 12′ N	94° 04′ E
Mipa	28° 37′ N	93° 18′ E
Molo	28° 54′ N	93° 53′ E
Mönda La	28° 29′ N	90° 36′ E
Mug	28° 09′ N	90° 59′ E
Mugu	28° 59′ N	91° 41′ E
Murchumo	30° 08′ N	94° 04′ E
Na La	28° 40′ N	93° 36′ E
Nambu Gompa	29° 59′ N	94° 28′ E
Nambu La	29° 59′ N	94° 19′ E
Namcha Barwa	29° 38′ N	95° 04′ E
Namdi	30° 00′ N	95° 00′ E
Nam La	29° 35′ N	95° 04′ E
Namla Karpo	30° 09′ N	94° 18′ E
Namse Gompa	29° 53′ N	93° 46′ E
Nanda	30° 07′ N	93° 32′ E
Nang Dzong	29° 03′ N	93° 10′ E
Nangartse Dzong	28° 59′ N	90° 25′ E
Nangtse	29° 46′ N	90° 47′ E
Natrampa	28° 21′ N	93° 06′ E
Nayu	29° 12′ N	94° 06′ E
Netang	29° 35′ N	90° 59′ E
Ningshi	29° 42′ N	94° 16′ E
Ningshi La	29° 53′ N	94° 22′ E
Nyala La	28° 08′ N	92° 13′ E
Nyarlu	29° 41′ N	94° 09′ E
Nye (Tsangpo Valley)	29° 01′ N	93° 17′ E
Nye (Yigrong Valley)	30° 25′ N	94° 00′ E
Nyerong	28° 23′ N	92° 50′ E
Nyima La	29° 38′ N	94° 52′ E
Nyoto Sama	30° 25′ N	93° 50′ E
Nyug La	28° 42′ N	94° 03′ E

Gazetteer of Ludlow and Sherriff Localities. Tibet (*cont.*)

Locality	Latitude	Longitude
Nyuksang (in Tsangpo Gorge)	29° 46′ N	95° 00′ E
Nyuri	27° 40′ N	92° 13′ E
Oka Dzong	29° 22′ N	92° 19′ E
Orong	29° 08′ N	93° 44′ E
Paka	29° 20′ N	94° 18′ E
Pa La	28° 46′ N	93° 42′ E
Palung	28° 58′ N	93° 33′ E
Pamse	28° 55′ N	93° 49′ E
Pang	30° 07′ N	93° 31′ E
Pang La (Tsari Dist.)	28° 40′ N	93° 37′ E
Pangchen	27° 41′ N	91° 48′ E
Pasum Kye La (Trasum Kye La)	30° 27′ N	93° 22′ E
Pasum Tso (Trasum Tso)	30° 01′ N	94° 00′ E
Pe	29° 31′ N	94° 53′ E
Pede	29° 08′ N	90° 27′ E
Pemakochung (in Tsangpo Gorge)	29° 45′ N	95° 05′ E
Penam Chu (at entrance to Pasum Tso)	30° 02′ N	92° 02′ E
Penda	30° 21′ N	94° 09′ E
Pen La	27° 58′ N	92° 15′ E
Pero La	29° 32′ N	95° 00′ E
Peru	28° 54′ N	93° 10′ E
Peteng (Pomé)	29° 57′ N	95° 20′ E
Peteng (Tsangpo Valley)	29° 12′ N	94° 04′ E
Phari Dzong	27° 43′ N	89° 10′ E
Podzo Sumdo	28° 41′ N	93° 28′ E
Pö La	27° 56′ N	91° 56′ E
Pomo Tso (on Eastern shore)	28° 35′ N	90° 30′ E
Potrang	28° 29′ N	93° 13′ E
Pumpatse	29° 43′ N	94° 48′ E
Pungkar Gompa	30° 17′ N	93° 31′ E
Putrang La	29° 03′ N	92° 22′ E
Rabdang	29° 06′ N	92° 51′ E
Ragoonka (Ragunka)	30° 25′ N	94° 20′ E
Ra La	28° 48′ N	92° 51′ E
Ralung	28° 50′ N	90° 03′ E
Rama	28° 18′ N	89° 40′ E
Raprang	28° 25′ N	93° 09′ E
Reting	30° 22′ N	91° 28′ E
Rham	28° 08′ N	89° 25′ E
Rib (Rip) La	28° 41′ N	93° 09′ E
Rimbu	28° 44′ N	93° 40′ E
Rongchakar (Rong)	29° 13′ N	92° 03′ E
Sakang (Sowgon)	28° 43′ N	89° 40′ E
Samoda	28° 23′ N	89° 33′ E
Sang	29° 29′ N	94° 41′ E
Sang La (Mönyul Dist.)	28° 09′ N	91° 58′ E
Sang La (Kongbo Dist.)	29° 35′ N	94° 43′ E
Sanga Chöling	28° 33′ N	93° 00′ E
Sanglung	29° 40′ N	95° 13′ E
Satang	29° 59′ N	95° 19′ E
Satang Peri	30° 00′ N	95° 25′ E
Sengdam	29° 45′ N	94° 57′ E
Senge Dzong (Tsangpo Gorge)	29° 47′ N	95° 03′ E
Senguti	28° 43′ N	93° 15′ E
Sera Gompa	29° 41′ N	91° 05′ E
Shacha Pebo	28° 42′ N	93° 55′ E
Shagam La	28° 36′ N	93° 18′ E
Shakti	27° 38′ N	91° 46′ E
Shangu La	28° 35′ N	93° 13′ E
Shi Dzong	29° 59′ N	93° 54′ E
Shinje Chögyal	29° 43′ N	94° 50′ E
Shio	28° 07′ N	92° 31′ E
Shirap	28° 38′ N	92° 38′ E
Shoga Dzong	29° 58′ N	93° 48′ E
Shoka	29° 14′ N	94° 10′ E
Shoka La	29° 07′ N	94° 16′ E
Showa Dzong	29° 55′ N	95° 25′ E
Showa La	29° 52′ N	95° 21′ E
Shu (Lisho)	29° 00′ N	93° 26′ E
Simbiteng	29° 11′ N	93° 56′ E
Simoneri	28° 39′ N	93° 09′ E
Singhi Dzong	28° 16′ N	90° 54′ E
Singo Samba	28° 48′ N	93° 56′ E
Sobhe La	30° 07′ N	94° 54′ E
Sokpo La	28° 41′ N	92° 57′ E
Su La	29° 49′ N	95° 24′ E
Sumbatse	28° 55′ N	93° 33′ E
Sur La	28° 46′ N	93° 11′ E
Takar La	28° 39′ N	93° 06′ E
Takpashiri (Chayul Dist.)	28° 11′ N	92° 51′ E
Takpashiri (Tsari Dist.)	28° 36′ N	93° 14′ E
Takpashiri (east of Migyitun)	28° 42′ N	93° 40′ E

Gazetteer of Ludlow and Sherriff Localities. Tibet (*cont.*)

Locality	Latitude	Longitude
Taktsa	28° 58′ N	93° 35′ E
Taktsang	28° 35′ N	93° 13′ E
Talung	28° 48′ N	90° 27′ E
Tama La	28° 35′ N	93° 17′ E
Tamnyen	29° 27′ N	94° 38′ E
Tamnyen La	29° 18′ N	94° 45′ E
Tana La	29° 54′ N	95° 07′ E
Tang	29° 43′ N	94° 02′ E
Tang La	27° 50′ N	89° 11′ E
Tangme	30° 07′ N	95° 08′ E
Tatti	29° 44′ N	93° 58′ E
Tawang	27° 34′ N	91° 56′ E
Temo Chamna	30° 15′ N	94° 56′ E
Temo Gompa	29° 30′ N	94° 30′ E
Temo La	29° 35′ N	94° 38′ E
Timpa	29° 33′ N	94° 52′ E
Tomtsang	28° 36′ N	93° 13′ E
Tonbe	30° 15′ N	95° 00′ E
Tongkyuk Dzong	29° 58′ N	94° 50′ E
Totsen	28° 43′ N	93° 17′ E
Towa Dzong	28° 23′ N	90° 49′ E
Trakan La	28° 43′ N	92° 45′ E
Trashijung	28° 45′ N	93° 53′ E
Tre	28° 05′ N	92° 06′ E
Trigu Dzong	28° 43′ N	91° 44′ E
Trigu Tso (middle of Lake)	28° 40′ N	91° 46′ E
Trimo	27° 55′ N	91° 54′ E
Trip (Sip)	29° 56′ N	94° 52′ E
Tripe	29° 37′ N	94° 56′ E
Tromda	29° 05′ N	92° 55′ E
Trön	28° 21′ N	93° 01′ E
Tro Shika	28° 16′ N	92° 34′ E
Truka La	27° 35′ N	92° 12′ E
Trulung	30° 03′ N	95° 03′ E
Tsakchugong	29° 53′ N	95° 09′ E
Tsanang La	29° 12′ N	94° 29′ E
Tsari Sama (an area or District)	28° 43′ N	93° 50′ E
Tse	29° 24′ N	94° 22′ E
Tsechen Gompa	28° 56′ N	89° 34′ E
Tsela Dzong	29° 26′ N	94° 22′ E
Tsemachi	28° 50′ N	93° 29′ E
Tsera	30° 03′ N	95° 13′ E
Tsetang	29° 15′ N	91° 51′ E
Tsobunang	28° 48′ N	93° 10′ E
Tsogo	30° 05′ N	94° 03′ E
Tso Kar	28° 40′ N	93° 42′ E
Tsona	28° 00′ N	92° 01′ E
Tulung La	27° 49′ N	92° 14′ E
Tumbatse	29° 40′ N	94° 47′ E
Tum La	29° 03′ N	94° 13′ E
Tuna	27° 58′ N	89° 13′ E
Tundo	29° 13′ N	94° 08′ E
Yang Tso	28° 28′ N	91° 44′ E
Yarap	28° 43′ N	93° 21′ E
Yar Shika	28° 14′ N	92° 40′ E
Yatung	27° 28′ N	88° 54′ E
Yigrong Tso (south end of Lake)	30° 12′ N	95° 00′ E
Yu La	28° 44′ N	93° 38′ E
Yum Tso	30° 00′ N	94° 12′ E
Yume	28° 39′ N	93° 08′ E
Yusum	29° 11′ N	94° 01′ E
Yuto	28° 40′ N	93° 07′ E
Zimsatti	28° 38′ N	93° 03′ E

Gazetteer of Ludlow and Sherriff Localities. Bhutan and Sikkim

Locality	Latitude	Longitude
Adung	27° 16′ N	90° 04′ E
Badar La	27° 34′ N	90° 47′ E
Balfai (Bulphai, *Griffith*)	27° 13′ N	91° 31′ E
Barshong (Parshong)	27° 42′ N	89° 33′ E
Batte Dzong	27° 15′ N	89° 25′ E
Bela La	27° 26′ N	89° 29′ E
Benkar (Trashigong Dzong; Benka, *Griffith*)	27° 18′ N	91° 34′ E
Black Mountain (Dunshinggang)	27° 17′ N	90° 24′ E
Bumdangtang (Bhoomlungtung, *Griffith*)	27° 36′ N	90° 50′ E
Bumtang (Byagur, *Griffith*)	27° 33′ N	90° 43′ E
Buxa	26° 45′ N	89° 36′ E
Byiti Sam	27° 12′ N	90° 40′ E
Chanana	27° 24′ N	89° 22′ E
Changpu (Bhutan-Mönyul Frontier)	27° 30′ N	91° 40′ E
Changsethang	27° 44′ N	90° 18′ E
Changu (Tsomgo)	27° 22′ N	88° 47′ E

Gazetteer of Ludlow and Sherriff Localities. Bhutan and Sikkim (*cont.*)

Locality	Latitude	Longitude
Chelai La (Cheli La)	27° 22′ N	89° 20′ E
Chenbi Rongang	27° 45′ N	91° 09′ E
Chendebi (Chindupjee, *Griffith*)	27° 27′ N	90° 20′ E
Chera La	27° 42′ N	92° 14′ E
Chesha La	27° 49′ N	90° 01′ E
Cheypechey	27° 57′ N	89° 28′ E
Chhukha Dzong (Chuka, *Griffith*)	27° 03′ N	89° 36′ E
Chizukang	27° 38′ N	90° 16′ E
Cho La	28° 03′ N	91° 46′ E
Chojo Dzong	27° 55′ N	90° 08′ E
Chöling La	27° 20′ N	91° 42′ E
Chorten Korra	27° 45′ N	91° 29′ E
Chumiten	27° 57′ N	89° 33′ E
Chungkar (Keri Gompa; Khegumpa, *Griffith*)	27° 03′ N	91° 27′ E
Chungsing	27° 03′ N	90° 34′ E
Chunzu Gompa	27° 13′ N	89° 30′ E
Damthang	27° 27′ N	89° 12′ E
Demri Chu	27° 07′ N	90° 34′ E
Denchung	27° 44′ N	91° 14′ E
Dhur	27° 37′ N	90° 41′ E
Dib La	27° 36′ N	91° 41′ E
Dikchu	27° 19′ N	88° 31′ E
Diwangiri	26° 52′ N	91° 30′ E
Dokyong La	27° 29′ N	89° 45′ E
Donga La (Doonglala, *Griffith*)	27° 34′ N	91° 19′ E
Donga Pemi	27° 34′ N	91° 17′ E
Donkya La	27° 59′ N	88° 47′ E
Dotena	27° 35′ N	89° 38′ E
Drugye Dzong	27° 30′ N	89° 19′ E
Dunkar La	27° 07′ N	90° 25′ E
Dungshinggang (Black Mountain)	27° 17′ N	90° 24′ E
Dunkhar	27° 50′ N	91° 07′ E
Dur Chutsen	27° 51′ N	90° 31′ E
Foomay	27° 48′ N	89° 56′ E
Gafoo La	27° 57′ N	90° 15′ E
Gale Chu	27° 05′ N	90° 30′ E
Gamri Chu (at junction with Dangme Chu)	27° 22′ N	91° 35′ E
Gangtok	27° 20′ N	88° 40′ E
Gnatong (Natang)	27° 18′ N	88° 50′ E
Goktang La	27° 48′ N	90° 34′ E
Gongte Gompa	27° 28′ N	90° 10′ E
Gufu	27° 25′ N	90° 12′ E
Gunisa	27° 38′ N	89° 15′ E
Gunkarah	27° 24′ N	91° 35′ E
Gyasa Dzong	27° 45′ N	89° 46′ E
Gyetsa (Jaisa, *Griffith*)	27° 30′ N	90° 39′ E
Ha	27° 22′ N	89° 18′ E
Ha La	27° 26′ N	89° 09′ E
Hamo	28° 05′ N	91° 08′ E
Hatisar	26° 53′ N	90° 30′ E
Hinglai La	27° 26′ N	89° 45′ E
Jelap La (Sikkim–Tibet Frontier)	27° 22′ N	88° 53′ E
Jigche La	27° 30′ N	90° 12′ E
Jirgang Chu (at junction with Mangde Chu)	27° 12′ N	90° 40′ E
Jiri Chu (source of stream near Balfai)	27° 13′ N	91° 31′ E
Jiu La	27° 47′ N	90° 35′ E
Jiutang	27° 53′ N	90° 32′ E
Julu	27° 48′ N	91° 14′ E
Kangchuka	27° 35′ N	90° 13′ E
Kangla Karchu La	27° 51′ N	89° 52′ E
Kang La	28° 00′ N	91° 13′ E
Kantanang	27° 47′ N	90° 46′ E
Kapcha Dzong (Chupcha, *Griffith*)	27° 12′ N	89° 34′ E
Karmu	Near Cho La	
Karponang	27° 23′ N	88° 38′ E
Khane (Khinay) Lhakang	27° 31′ N	91° 06′ E
Khem La	27° 46′ N	90° 24′ E
Kheri Gompa (Khegumpa, *Griffith*)	27° 03′ N	91° 27′ E
Khoma Chu (at junction with Kuru Chu)	27° 39′ N	91° 12′ E
Khomanagri (Khoomun, *Griffith*)	27° 08′ N	91° 26′ E
Kinga Rabden	27° 24′ N	90° 30′ E
Kitipu	27° 34′ N	90° 42′ E
Kohina	27° 49′ N	89° 48′ E

Gazetteer of Ludlow and Sherriff Localities. Bhutan and Sikkim (*cont.*)

Locality	Latitude	Longitude
Kulong Chu (Koolong ; at junction with Manas River)	27° 26′ N	91° 37′ E
Kumathang	27° 44′ N	89° 22′ E
Kyipup	27° 21′ N	88° 51′ E
Kyi-kyi La	27° 33′ N	90° 41′ E
Kyü La	27° 26′ N	89° 07′ E
Lachen	27° 44′ N	88° 33′ E
Lachung	27° 42′ N	88° 45′ E
Lagyap (Laghep)	27° 22′ N	88° 42′ E
Lamse La	27° 25′ N	90° 15′ E
Lao	27° 52′ N	91° 28′ E
Lao La	27° 32′ N	90° 09′ E
Lap	27° 40′ N	92° 15′ E
Laya	27° 54′ N	89° 48′ E
Leji	27° 52′ N	90° 06′ E
Lhuntse Dzong	27° 39′ N	91° 10′ E
Lingshi Dzong	27° 55′ N	89° 27′ E
Lingshi La	27° 57′ N	89° 27′ E
Linji (Lingitsi ; Linje, *Griffith*)	27° 36′ N	91° 13′ E
Lometsawa	27° 31′ N	89° 48′ E
Longte Chu (at junction with Mangde Chu)	27° 26′ N	90° 29′ E
Loona (district near Leji)	27° 48′ N	90° 00′ E
Lubsing La	27° 47′ N	90° 45′ E
Lungur	27° 47′ N	92° 14′ E
Mago (district in which Nyuri and Dyuri are the principal localities)	27° 40′ N	92° 10′ E
Mangde Chu (Trongsa Chu)	River about	90° 40′ E
Mara Chu (at junction with Mo Chu)	27° 12′ N	90° 00′ E
Marlung	27° 56′ N	90° 38′ E
Marutang	27° 35′ N	90° 16′ E
Me La	27° 58′ N	91° 37′ E
Mem La	27° 39′ N	89° 21′ E
Menjibi	27° 33′ N	91° 10′ E
Menoka Tea Estate	26° 45′ N	91° 30′ E
Mera	27° 19′ N	91° 50′ E
Mo Chu	River on which Punaka is situated	
Mon La	27° 05′ N	90° 37′ E
Mön La Karchung La	28° 05′ N	90° 39′ E
Mönle La	27° 24′ N	89° 59′ E
Muktur	27° 32′ N	91° 58′ E
Nabzi	27° 08′ N	90° 29′ E
Naha	27° 45′ N	89° 29′ E
Namda La	27° 51′ N	90° 34′ E
Namdating	27° 52′ N	90° 32′ E
Narimthang	27° 57′ N	91° 13′ E
Natang (Gnatong)	27° 18′ N	88° 50′ E
Natu La (Sikkim–Tibet Frontier)	27° 23′ N	88° 50′ E
Nelli La	27° 51′ N	89° 23′ E
Nyingsang La	27° 27′ N	91° 55′ E
Nyongchung La	28° 02′ N	92° 05′ E
Nyuksang La	27° 20′ N	91° 53′ E
Omta Tso	27° 37′ N	90° 17′ E
Oke La	28° 10′ N	90° 02′ E
Okse La	27° 06′ N	90° 29′ E
Orka La	27° 23′ N	92° 01′ E
Padima Tso	27° 42′ N	90° 21′ E
Pang La (West Bhutan)	27° 45′ N	89° 22′ E
Pang La (East Bhutan)	27° 44′ N	91° 18′ E
Pangotang	27° 50′ N	90° 42′ E
Pangte La	27° 45′ N	89° 22′ E
Paro	27° 25′ N	89° 25′ E
Passu Sepo	27° 57′ N	90° 22′ E
Pedong	27° 09′ N	88° 38′ E
Peipe La	27° 40′ N	90° 48′ E
Pele La	27° 32′ N	90° 12′ E
Pemionchi (Pemayangtse)	27° 18′ N	88° 15′ E
Pemitanka	27° 26′ N	89° 32′ E
Phadonchen (Sedonchen)	27° 14′ N	88° 46′ E
Phage La	27° 49′ N	90° 25′ E
Phalut	27° 12′ N	88° 01′ E
Pho Chu	Large river joining the Mo Chu at Punaka	
Phobshika	District near the Black Mountain	
Phongmi	27° 23′ N	91° 45′ E
Pimi (Pémee, *Griffith*)	27° 34′ N	90° 59′ E
Pü La or Pö La or Bod La	28° 02′ N	91° 14′ E
Puduna	27° 20′ N	89° 18′ E
Pumo La	27° 27′ N	89° 35′ E

Gazetteer of Ludlow and Sherriff Localities. Bhutan and Sikkim (*cont.*)

Locality	Latitude	Longitude
Punaka (Punukha, *Griffith*)	27° 36′ N	89° 51′ E
Pung La	27° 41′ N	91° 12′ E
Rangpo	27° 11′ N	88° 32′ E
Rhenok	27° 10′ N	88° 38′ E
Ridang (Rydang, *Griffith*)	27° 34′ N	90° 10′ E
Rinchen Chu (source in Thampe La)	27° 40′ N	90° 17′ E
Rip La	27° 42′ N	91° 13′ E
Rocha Chu (at junction with Kulong Chu)	27° 34′ N	91° 30′ E
Rongli (Rangli)	27° 12′ N	88° 41′ E
Ronglung (Roongdong, *Griffith*)	27° 15′ N	91° 34′ E
Rudo La (Rodoola, *Griffith*)	27° 35′ N	90° 55′ E
Rukubi	27° 29′ N	90° 18′ E
Rungzyung	27° 22′ N	91° 40′ E
Saga La (West Bhutan)	27° 28′ N	89° 17′ E
Saga La (Central Bhutan)	27° 54′ N	90° 26′ E
Sakden	27° 24′ N	91° 54′ E
Samtegang (Santagoung, *Griffith*)	27° 31′ N	90° 01′ E
Sana (Sanah, *Griffith*)	27° 34′ N	91° 25′ E
Sandakphu	27° 07′ N	88° 01′ E
Sang La	28° 09′ N	91° 58′ E
Sassi (Sassee, *Griffith*)	27° 08′ N	91° 27′ E
Satsalor	26° 56′ N	91° 29′ E
Sawang	27° 42′ N	91° 14′ E
Sebu La	28° 08′ N	88° 36′ E
Sedonchen	27° 14′ N	88° 46′ E
Sefu	27° 32′ N	90° 19′ E
Sergong La	27° 52′ N	91° 03′ E
Shabjetang	27° 39′ N	90° 43′ E
Shali	27° 29′ N	91° 35′ E
Shambling	27° 46′ N	91° 09′ E
Shamgong Dzong	27° 14′ N	90° 39′ E
Shapang	27° 39′ N	91° 27′ E
Sharitang	27° 25′ N	89° 02′ E
Shimitang	27° 46′ N	90° 43′ E
Shingbe	27° 55′ N	91° 33′ E
Shinje La	27° 58′ N	89° 39′ E
Shole La	27° 25′ N	90° 06′ E
Sibsi La	27° 40′ N	91° 20′ E
Singtam	27° 14′ N	88° 30′ E
Singhi Dzong	27° 55′ N	91° 13′ E
Surelakha	27° 01′ N	90° 32′ E
Taglung La	27° 41′ N	89° 21′ E
Takila	27° 34′ N	91° 12′ E
Takse	27° 20′ N	90° 37′ E
Taktoo	27° 23′ N	91° 47′ E
Tamachu (Tumashoo, *Griffith*)	27° 34′ N	91° 11′ E
Tang Chu (at Mo Chu junction)	27° 28′ N	89° 54′ E
Tangnaru	27° 36′ N	90° 53′ E
Tanglu	27° 02′ N	88° 07′ E
Telegang (Tolegang)	27° 49′ N	90° 40′ E
Thampe La	27° 40′ N	90° 17′ E
Thampe Tso	27° 41′ N	90° 19′ E
Thang (Tang)	27° 35′ N	90° 52′ E
Thimbu Chu	Tributary of Wong Chu near Trashi Chö Dzong	
Thita Tso	27° 38′ N	90° 18′ E
Tibdey La	27° 24′ N	90° 42′ E
Timnyung Dzong	27° 41′ N	91° 10′ E
Tobrang	27° 45′ N	91° 28′ E
Tosumani	27° 51′ N	91° 15′ E
Tranza (Tranzo)	27° 57′ N	90° 09′ E
Trashigong Dzong (Benka, *Griffith*)	27° 18′ N	91° 34′ E
Trashiyangtse Dzong (Tassyassy or Tassangsee, *Griffith*)	27° 34′ N	91° 20′ E
Trashi Chö Dzong (Thimbu; Tassisudon, *Griffith*)	27° 29′ N	89° 38′ E
Trashiling (Tasseling, *Griffith*)	27° 27′ N	90° 27′ E
Trongsa Dzong	27° 31′ N	90° 31′ E
Tsalimape	27° 26′ N	89° 39′ E
Tsampa	27° 49′ N	90° 43′ E
Tsanka	27° 29′ N	90° 28′ E
Tsele La	27° 25′ N	90° 10′ E
Tseli La	27° 14′ N	89° 16′ E
Tunle La	27° 27′ N	90° 37′ E

Gazetteer of Ludlow and Sherriff Localities. Bhutan and Sikkim (*cont.*)

Locality	Latitude	Longitude
Ungar (Oongar, *Griffith*)	27° 33′ N	91° 02′ E
Waitang (Weitang)	27° 55′ N	90° 45′ E
Wangdi Potrang (old spelling Angdu Phorang, Wandipore, *Griffith*)	27° 28′ N	89° 54′ E
Woji	27° 51′ N	89° 57′ E
Worthang	27° 54′ N	90° 28′ E
Yale La	27° 52′ N	89° 26′ E
Yari La	28° 00′ N	89° 36′ E
Yönpu La	27° 13′ N	91° 35′ E
Yuto La	27° 31′ N	90° 35′ E

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RELIQUIAE BOTANICAE HIMALAICAE

By FRANK LUDLOW

SUMMARY

Androsace nortonii (Primulaceae), *Corydalis brevicalcarata, C. sherriffii* (Papaveraceae), *Cremanthodium bhutanicum, C. campanulatum* var. *pinnatisectum* (Compositae), *Geum macrosepalum* (Rosaceae), *Haplosphaera himalayensis* (Umbelliferae), *Saussurea neglecta* (Compositae) and *Senecio kongboensis* (Compositae) from the Himalayas and adjacent south-eastern Tibet are new. *Geum versipatella* Marquand is considered conspecific with *G. sikkimense* Prain, the protologue of which covered two species, *G. sikkimense* (for which a lectotype is designated here) and *G. macrosepalum.* The flowers of *Diapensia wardii* W. E. Evans, originally based on non-flowering material, are described.

INTRODUCTORY NOTE

Frank Ludlow (1885–1972) devoted most of the last twenty years of his life to the study of the large botanical collections which he and George Sherriff had amassed during their expeditions to Bhutan and south-eastern Tibet between 1933 and 1950. Whenever possible these plants were put into the hands of specialists for naming, P. C. Tsoong, for example, dealing with *Pedicularis*, T. T. Yü and G. Klotz with *Cotoneaster*, H. Smith with *Saxifraga* and *Gentiana*, J. L. van Soest with *Taraxacum*, P. H. Raven with *Epilobium*, W. T. Stearn with *Allium*, H. Hara with *Chrysosplenium*, W. W. Smith and H. R. Fletcher with *Primula* and Frances Balfour-Browne with Fungi. Ludlow himself, with the help of the botanical staff of the British Museum (Natural History), determined most of those remaining. This necessitated their comparison with material from adjacent regions, notably Sikkim, Nepal and western China, and led to the recognition of many new species. Ludlow published some of them under the title 'Novitates Himalaicae' in *Bull. Br. Mus. nat. Hist.* (Bot.) **2** : 65–78 (1956). At the time of his death he had prepared descriptions and notes on yet others. These are published below with a few minor emendations and additions. Figs 4, 5 and 7 were drawn by Mr D. Erasmus, Figs 8 and 9 by Miss Victoria Goaman, Figs 2 and 6 by Miss E. M. Stones. The specimens cited are in the British Museum (Natural History) unless stated otherwise.

W. T. Stearn

GEUM SIKKIMENSE AND ALLIED SPECIES (ROSACEAE)

The three Himalayan species discussed below differ from *Geum* proper, with *G. urbanum* L. as lectotype, in having straight styles and belonging to the group sometimes generically separated from *Geum*, e.g. by Greene (1906), Rydberg (1913), F. Bolle (1933) and Hutchinson (1964), under the name *Acomastylis* Greene, with *Sieversia rossii* R. Br. (*Geum rossii* (R. Br.) Seringe) as lectotype. In *Geum* proper the style is differentiated into a lower (proximal) part and an upper (distal) part by a sigmoid bend; as the achene matures the upper part breaks off at the bend, leaving the lower part with a hooked tip which becomes rigid and aids dispersal of the achene by catching on to the fur of mammals. However, a number of species commonly included in *Geum* have completely persistent styles and the three Himalayan species do not appear closely related to the Arctic species placed in *Acomastylis*. It would seem that more information is to be lost than gained by dividing *Geum* into several small genera ; moreover, W. Gajewski, 'A cytogenetic study of the genus *Geum*' (*Monographiae Bot.* **4** : 1–416 (1957)) keeps *Geum* intact while recognizing eleven subgenera. These species are accordingly here retained in *Geum*.

An examination of the type-sheets of *Geum sikkimense* Prain at Kew revealed that two species, not one, are involved. This species was originally founded on three gatherings, all from western Sikkim. Two of these were made by King's collector, one at Onglathang near Jongri in 1887, the other in the following year at an unspecified locality. The third gathering was made in September 1901, at a place called Hewalungi (spelt Huhalanghi in the text) by Prain's own collector. Although this third gathering is in fruit, the calyx, corolla and stamens still persist, and these suffice to show that this plant is very different from that obtained by King. For whereas in King's plant the calyx lobes are triangular, the petals hairy only at the base, and the stamens 3–4 mm in length, in Prain's plant the calyx lobes are broadly ovate, the petals hairy on the outside from base to apex, and the stamens 7–8 mm long. The chief difference, however, lies in the style, which in Prain's plant is almost entirely deciduous, whereas in King's plant (as is evident from maturer gatherings than those obtained by King) the whole style is persistent.

The description and illustration of *G. sikkimense* in *J. Asiat. Soc. Beng.* **73**(2) : 200, t.7 (1904) were clearly based on all three gatherings cited by Prain. The differences in calyx between the flowering and fruiting collections he obviously accepted as being due to development after flowering. Other differences he accepted as being due to variation. Prain did not mark any of the gatherings as type, but since the major part of his description and also most of the illustration is of the flowering material collected for King, it is reasonable to select a lectotype from this ; it is therefore proposed that the sheet in the Kew Herbarium marked 'Dr. King's Collector, June 1887', which is inscribed 'Geum sikkimense Prain in Journ. As. Soc. Beng. LXXIII. 200' in Prain's own hand, shall be the lectotype of that name. This being so, a new name must be found for the fruiting specimen from Hewalungi. Fortunately, of recent years, Ludlow and Sherriff, Kingdon-Ward, and Cooper have all collected Prain's plant on several occasions in Bhutan, Assam and south-eastern Tibet, so that ample material is now available for the description of this new species here named *G. macrosepalum*.

The three Himalayan species of *Geum* with straight styles may be distinguished as follows :

Terminal leaflet of basal leaves scarcely longer and not much broader than lateral leaflets . . . . 3. *G. elatum*
Terminal leaflet of basal leaves very much longer and broader than lateral leaflets :
  Sepals 3–6 mm broad, green ; petals glabrous . . . 2. *G. sikkimense*
  Sepals 8–10 mm broad, almost the same colour as the petals ; petals hairy 1. *G. macrosepalum*

The only other Himalayan species of *Geum* is *G. roylei* Wall. ex F. Bolle in *Beih. Repert. nov. Spec. Regni. veg.* **72**: 66 (1933), the Himalayan counterpart of the European and Western Asiatic *G. urbanum* L., which has the style bent sigmoidally in flower and the achenes hooked at the tip of the persistent style-base. This ranges from Chitral and Kashmir to Central Nepal.

1. ***Geum macrosepalum*** Ludlow, sp. nov. (Plate 30A; Text-fig. 2.)

Herba perennis usque ad 50 cm alta, *rhizomate* praemorso lignoso adscendente, plusminusve 2 cm longo et 1 cm diametro, *caulibus* simplicibus erectis puberulis. *Folia radicalia* 6–10, conferta, lyrata, herbacea, utrinque pilosa, 6–18 cm longa, usque ad 4–5 cm lata, ambitu obovati-oblonga, basin versus angustata, simpliciter pinnata, lobis 5–10 jugis; lobus terminalis late ovatus vel subcircularis vel reniformis, 2–5 cm longus et 2–4·5 cm latus, marginibus crenati-dentatis; lobi laterales minuti, sessiles, circulares, marginibus crenati-dentatis. *Folia caulina* 2–4, utrinque subhispida, sessilia, ambitu obovata vel late oblanceolata, 1–4 cm longa, 0·5–2 cm lata, marginibus dentatis; *stipulae* binae oppositae, foliaceae, ambitu ovatae, 1–1·5 cm longae et plusminusve 1 cm latae, marginibus serrati-dentatis.

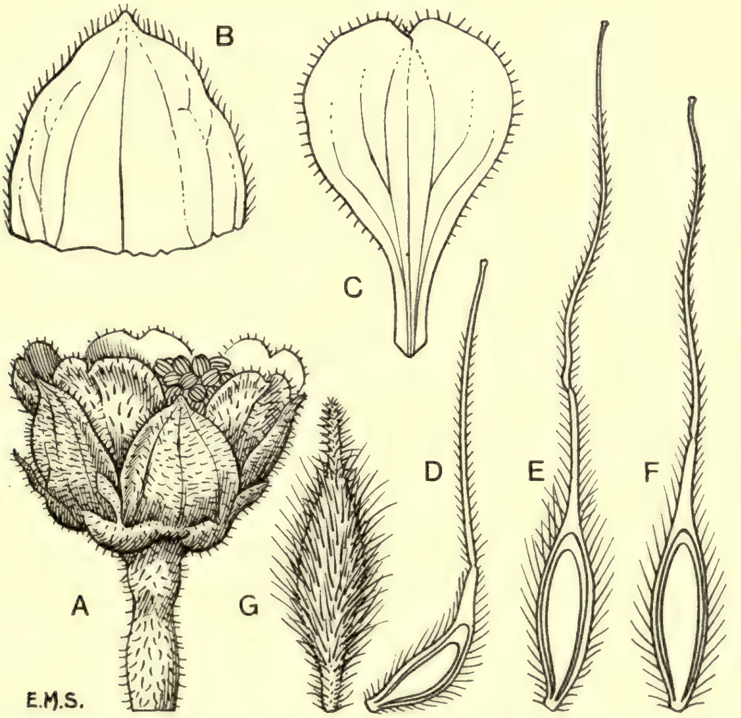

FIG. 2. *Geum macrosepalum* Ludlow; A, flower (*L & S 19171*, holotype), ×2; B. sepal (*L & S 19171*), ×4; C, petal (*L & S 19171*), ×4; D–F, gynoecium (D. E, *L & S 1684*; F, *Kingdon-Ward 12002*), ×8; G, mature achene (*Prain's collector 204*), ×8.

Flores solitarii rare bini, usque ad 3 cm diametro. *Bracteolae* 5, lanceolatae, 5–6 mm longae, hispidae. *Calyx* 5-lobatus, coloratus, luteus, flavo-virens vel fulvus; lobi ovati ad late ovati, 1–1·5 cm longi, 0·8–1 cm lati, apiculati, extus hispidi intus glabri. *Petala* 5, lutea fulva flava eburneave, obovata, basi unguiculata, apice retusa ad emarginata, 1–1·2 cm longa, 0·6–0·7 cm lata, extus praecipue apicem versus pilosa. *Stamina* numerosa (50–80); *antherae* ellipticae, plusminusve 0·8 mm longae; *filamenta* 6–10 mm longa, basi libera, apicem versus pilosa, gracillima. *Receptaculum* conicum, basi plusminusve 4 mm longum et 4 mm latum. *Carpella c.* 70; *stylus* porrectus, 6–10 mm longus, hirsutus, gracilis, apicem versus gradatim attenuatus, supra basin constrictus, parte superiore in statu maturo decidua. *Achenia* ellipsoidea, in statu maturo 5–6 mm longa, brevissime pedunculata, apice rostro 1–2 mm longo instructa, plusminusve dense hirstua.

SIKKIM: Hewalungi, September 1901, *Prain's collector 204* (K).

BHUTAN: Rinchen Chu (27° 38′ N, 90° 17′ E), 4200 m, 'common on open stony hillside; corolla pale yellow, calyx lemon yellow to red yellow', 5 July 1937, *Ludlow & Sherriff 3389*. Saga La, Upper Mangde Chu (27° 55′ N, 90° 25′ E), 4200 m, 'grassy alpine slopes; calyx red green or green, corolla ditto', 14 July 1949, *Ludlow, Sherriff & Hicks 16824*. Pangothang, Tsampa (27° 50′ N, 90° 42′ E), 4200 m, 'flowers dull yellow, calyx greenish yellow', 16 June 1949, *Ludlow, Sherriff & Hicks 19171* (holotype in Herb. Brit. Mus.). Shingbe, Me La, (27° 56′ N, 91° 33′ E), 3800–4200 m, 6 June 1949, *Ludlow, Sherriff & Hicks 20322*. Parshong Timpu (27° 42′ N, 89° 34′ E), 4000 m, 'flowers white', 27 July 1914, *Cooper 1963*.

ASSAM: Luguthang (27° 32′ N, 92° 11′ E), 4000 m, 'flowers scarcely open, white or yellow', 6 June 1935, *Kingdon-Ward 11639*.

S.E. TIBET: Lang La (28° 58′ N, 93° 42′ E), 4200 m, 'flowers yellow or reddish', 16 July 1935, *Kingdon-Ward 12002*. Takar La, Tsari (28° 40′ N, 93° 05′ E), 4000 m, 'corolla pale lemon yellow, calyx lemon green', 27 June 1936, *Ludlow & Sherriff 2226*. Langong (28° 51′ N, 93° 47′ E), 4400 m, 'corolla pale lemon yellow, calyx slightly darker', 28 May 1938, *Ludlow, Sherriff & Taylor 3899*.

Several characters distinguish this new species from other Himalayan members of the genus. The most important are (a) large broad ovate calyx lobes which are almost the same colour as the petals; (b) petals which are hairy on the outside from base to apex; (c) stamens varying in length from 6 to 10 mm according to age; (d) a jointed style, the greater part of which is deciduous.

2. **Geum sikkimense** Prain in J. Asiat. Soc. Beng. 73 : 200, t. 7 (1904).

Acomastylis sikkimensis (Prain) F. Bolle in Beih. Repert. nov. Spec. Regni veg. **72** : 83 (1933).

Geum versipatella Marquand in Curtis's Bot. Mag. 157 : t. 9344 (1934).

NEPAL: Tukucha, Kali Gandaki Valley, 3500 m, 15 June 1954, *Stainton, Sykes & Williams 1152, 1154*. Larjong (S. of Tukucha) 3000 m 'calyx and filaments green, petals reddish white', 23 July 1954, *Stainton, Sykes & Williams 1953*. Sauwala Khola 3600 m, 4 June 1954, *Stainton, Sykes & Williams 2976*. Rambrong, Lamjung

Himal, 4000 m 'petals cream', 1 July 1954, *Stainton, Sykes & Williams 6057*. S. of Khola Kharka, 4250 m, 'flowers white', 15 July 1949, *Polunin 1062*. Tangba, 4250 m, *Lall Dhwoj 216*. Michet, 4500 m, *Lall Dhwoj 78*.

SIKKIM: Onglathang near Jongri, June 1887, *King's Collector* (lectotype of *G. sikkimense*, K).

BHUTAN: Tang Chu, Ritang, Central Bhutan, 3600 m, 'corolla white, back of petals sometimes pink', 6 June 1937, *Ludlow & Sherriff 3194*. Rinchen Chu, Central Bhutan, 3600–4000 m, 'corolla pink to very pale pink', 4 July 1937, *Ludlow & Sherriff 3382*. Thita Tso, Central Bhutan, 4000 m, 'corolla reddish pink with a lot of white internally and towards the base', 10 August 1949, *Ludlow, Sherriff & Hicks 17097*.

When Marquand described *Geum versipatella* he stated that it differed from its most closely allied species 'in the flowers being white instead of yellow, in the much longer pedicels and in having rather more numerous stamens with longer filaments'.

When examining the numerous gatherings in the British Museum (Natural History) which seemed to agree completely with the type material of *G. sikkimense* at Kew, I noticed that none had yellow flowers, and that all had white or pinkish-white flowers. Since the colour of the flowers is not mentioned on King's sheet of *G. sikkimense* at Kew, or on those in the Calcutta Herbarium, it seems possible that Prain erred in describing the flowers as yellow. The flowers *look* yellow in King's type, it is true, but they also look yellow in white-flowered specimens collected in recent years in Nepal and Bhutan. As already remarked, Prain erroneously associated the yellow-flowered plant obtained by his collector at Hewalungi with *G. sikkimense* and in the absence of any note on the colour of the flowers in King's specimens he may well have assumed that they were likewise yellow. The greater length of the pedicels in *G. versipatella* appears unimportant. Ten sheets of this plant in the British Museum (Natural History) with white or pinkish-white flowers have pedicels varying in length from 1 cm to 8 cm. As regards the stamens Marquand states that in *G. versipatella* the filaments are 'up to 4 mm long'. In the ten gatherings mentioned the filaments are 3–4 mm long, the older plants tending to have longer filaments. Prain gives no filament measurement for *G. sikkimense*. Actually in the type material the filaments are just over 3 mm long, though the illustration by the Indian artist shows them to be over 4 mm long. It can hardly be said, therefore, that the filaments in *G. versipatella* are appreciably longer than they are in *G. sikkimense*. Prain gives 40–50 as the total number of stamens in *G. sikkimense*. Marquand states that the stamens in *G. versipatella* are 'very numerous (exceeding 50)'. The number of stamens in *Dhwoj 216*, which Marquand cites as being equivalent to *G. versipatella*, is over 100, and in the ten gatherings with white or pinkish-white flowers in the British Museum (Natural History) the number varies from 80 to 115, often over 100. Prain almost certainly under-estimated the number of stamens in King's gathering of *G. sikkimense*, for in one of the flowers on the type sheet it is possible to count over 50 filaments, and others would undoubtedly come into view if dissection were made. Since dissection would injure the type, a gathering, *Ludlow & Sherriff 3194*, from Bhutan was chosen as being an almost exact replica of King's type and here the number of stamens on dissection was found to be over 100.

There remains the poise of the flower. Marquand states, and his illustration shows, that the flowers in *G. versipatella* face downwards. Prain states that the flowers in *G. sikkimense* are erect. In the field notes accompanying the ten white-flowered gatherings in the British Museum (Natural History) there is no mention of nodding flowers, and as far as it is possible to judge from dried material most appear to have been erect. But plants with long pedicels collected in the autumn *do* appear to have had flowers which faced downwards. Moreover, the photograph of *G. sikkimense* in Hara & others, *Spring Flora of Sikkim Himalaya*, fig. 94 (1963) shows an almost nodding flower.

In short, all the evidence indicates that *G. versipatella* Marquand is conspecific with *G. sikkimense* Prain.

3. ***Geum elatum*** Wall. ex G. Don, Gen. Syst. Gard. Bot. 2 : 526 (1832). – Hook. f., Fl. Brit. Ind. 2 : 343 (1878).

Geum elatum Wall., Numer. List : 21, no. 711 (1829) ; nomen nudum.
Sieversia elata Royle, Illustr. Bot. Himal. : t. 39 f. 1 (Sept. 1834), p. 207 (April 1835).
Acomastylis elata (Wall.) F. Bolle in Beih. Repert. nov. Spec. Regni, veg. 72 : 83 (1933).

In a 'Note on the varieties of *Geum elatum*, Wallich' (*Notes R. bot. Gdn Edinb.* **14** : 27–30 ; 1923), W. E. Evans pointed out that the specimens listed under the number Wall. Cat. 711, consist of two distinct gatherings, one by Robert Blinkworth from Kumaun and the other by Dr Govan from Sirmore, and that the achenes in these two gatherings are either hispid or almost glabrous. He suggested that it was likely that all specimens from one of these localities (it was impossible to say which) had either hispid or glabrous achenes, and he proposed epithets (1) var. *typicum* and (2) var. *leiocarpum* for these variants respectively. Royle figured the achene as hispid and stated that it had a 'hairy achenium'. Examination of the abundant material of *G. elatum* in the herbarium of the British Museum (Natural History) does not support Evans' view. On nine occasions both hispid and glabrous achenes have been found in plants of the same gathering, though not on the same plant. Had this happened once, or even twice, it would have been reasonable to conclude that the gatherings had become mixed, but it is impossible to believe that this could have happened on nine different occasions. The hispid or glabrous nature of the achenes in *G. elatum* is not therefore important enough to warrant varietal distinction. Moreover there are intermediate stages. In some instances the achenes are neither hispid nor completely glabrous but show a limited amount of hairiness at the apex. Evans' plate CXCV illustrating *G. elatum* var. *typicum* W. E. Evans is from a duplicate of Blinkworth's gathering in the Hooker Herbarium at Kew. In the Wallich Herbarium at Kew there are two Blinkworth sheets from Kumaun and two Govan sheets from Sirmore. In all four sheets the achenes, as far as can be seen, are hispid, and this state seems to be far commoner than the glabrous state. Royle's private herbarium is at Liverpool (cf. Stansfield in *Liverpool Bull.* **3** : 5–38 ; 1954), and through the courtesy of Mr H. Stansfield, Keeper of Botany, City Museum, Liverpool, I have been able to examine the *Geum* material which Royle collected. There are four gatherings in all, and one of these, no. 64/30 from Kedarkanta, in all probability formed the basis of his description of *Sieversia elata*. Royle originally gave this plant the manuscript name of *Geum grandiflorum* and this name is also written in Urdu on the back of his label. Later, probably after he had compared his own gathering with material in the Wallich Herbarium, he added in pencil '*G. elatum* Wall. 711'. All the achenes in Royle's gatherings are hairy, thus agreeing with his description and illustration.

G. elatum var. ***humile*** (Royle) Hook. f., Fl. Brit. Ind. 2 : 343 (1878). – W. E. Evans in Notes R. bot. Gdn Edinb. 14 : 28, t. 196 (1923)

Geum adnatum Wall., Numer. List. : 21, no. 712 (1829) ; nomen nudum.
Sieversia elata var. *humilis* Royle, Illustr. Bot. Himal. : 207 (1835).
Potentilla adnata Wall. ex Lehm., Nov. Minus Cogn. Stirp. Pug. 9 : 9 (1851).–Lehm., Revis. Potentill. : 47, t. 17 (1856), reimpr. ex Nova Acta Acad. Caes. Leop. Carol. 23, Suppl. (1856).
Acomastylis elata var. *humilis* (Royle) F. Bolle in Beih. Repert. nov. Spec. Regni veg. 72 : 84 (1933).

In Royle's herbarium at Liverpool there is a gathering of a *Sieversia*, no. 64/31, collected at Shalma in the Tons Valley north of Mussoorie. Unfortunately it is in a somewhat imperfect state. Originally there was a single flower head but this has been broken off, and the flowering stem has become detached from the parent plant. Nevertheless it is highly probable that this specimen is the true type of Royle's *Sieversia elata* var. *humilis*. The label in Royle's handwriting shows that, at first, he identified this plant with *Geum montanum* and that name appears also in Urdu on the back of the label. Subsequently he scored out the epithet *montanum* and replaced it by *auriculatum*. Finally he wrote on the label the words 'An sieversiana' in pencil. On the left-hand side of the label is a mysterious pencil sketch of an achene with a looped style, which is certainly not that of *Sieversia* but resembles that of *Geum urbanum* L. There are two gatherings of '*G. urbanum*' (i.e. *G. roylei*) in Royle's herbarium, no. 64/29 from Choor, Nagkunda and no. 64/32 from Kashmir, but both these gatherings have their own correct labels written by Royle himself. Whatever the explanation of this pencilled drawing may be, there can be no doubt that this Shalma gathering is *Sieversia elata* in respect of its leaves and stem, and accords with his description of var. *humilis* 'caule unifloro, foliisque minoribus'.

At Kew, in the Hooker Herbarium, there is a sheet of *Sieversia elata* Royle on which, in addition to the typical plant, there has been mounted a specimen of var. *humilis* (though not named as such) with a flowering stem bearing a single open flower, and two undeveloped buds. The stem in this specimen, as in that of the Shalma plant, is longer than the leaves. Unfortunately the flower has been mounted face downwards so that it is impossible to say whether the achenes are hispid or glabrous. *G. adnatum* Wall. Cat. 712 from Gossain Than, Nepal, appears to have had hispid achenes in the one flower where they are visible. There are also specimens of *G. adnatum* in the Bentham Herbarium where the achenes are glabrous, and in the

Hooker Herbarium where they are not visible. Neither of these sheets is marked as a duplicate of *Wall.* 712, though probably both are of the same collecting. In Hooker's own gathering of *G. elatum* var. *humile* at Yumthan in upper Sikkim, and in Norton's sheet from Karma near Everest, the achenes are hispid. In the British Museum (Natural History), Herbarium, on a sheet from Sikkim collected by King, the achenes are again hispid, but on a sheet from Nepal collected by Bailey they are glabrous. The flowering stems are sometimes no longer than the radical leaves but more often they are longer, and though the flowers are generally solitary, stems bearing 2–3 flowers may occur. Altogether var. *humile* seems little more than a dwarf alpine state of *G. elatum.*

G. elatum forma ***rubrum*** Ludlow, forma nov. (Plate 30B.)

A typo (forma *elato*) petalis filamentisque rubris differt.

KASHMIR : Bangas, Kaj Nag Range, *Miss Carmichael* s.n. (Herb. Kew).

NEPAL : Babaria Lekh, 3650 m, 29 May 1952, 'open moorland, flowers bright red', *Polunin, Sykes & Williams 2115.* Hills south of Jumla, 3500 m, 2 July 1952, 'petals bright red, filaments red', *Polunin, Sykes & Williams 4419* (holotype in Herb. Brit. Mus.). Maharigaon, 4400 m, 13 July 1952, 'growing abundantly on grassy slopes, flowers bright red', *Polunin, Sykes & Williams 141.* Sirtibang Lekh, 3500 m, 11 July 1954, *Stainton, Sykes & Williams 3454.* Sirtibang Lekh, 3500 m, 14 October 1954, 'seed and live roots collected', *Stainton, Sykes & Williams 9020.*

This is a particularly handsome colour form of *Geum elatum.* According to the collectors, it grows abundantly on grassy slopes and open moorland above tree level between 3500 and 4250 m, and does not appear to be mixed with the typical yellow-flowered plant in its natural state. It is now in cultivation in Britain having been introduced from Nepal in 1954 under S.S.W. 9020. Although in the wild state the flowers are said by the collectors to be either deep red or scarlet and not to exhibit intermediate colour phases, this is not so in cultivation where deep orange or apricot flowers frequently occur.

J. R. Sealy and W. T. Stearn have greatly helped me in the preparation of these notes.

HAPLOSPHAERA (UMBELLIFERAE)

Haplosphaera himalayensis Ludlow, sp. nov. (Plate 31, Text-fig. 3.)

Herba perennis, erecta. *Radix* descendens, parce ramosa, circiter 50 cm longa, collum versus 1–1·5 cm crassa, ad apicem folia marcida anni praecedentis gerens. *Caulis* erectus, sulcatus, fistulosus, usque ad 120 cm altus, basi 0·75–1 cm crassus. *Folia basalia* numerosa ; petiolus laminam aequans vel ea parum brevior, 10–15 cm longus, basi longe vaginatus et leviter inflatus ; lamina ambitu ovato-triangularis tri-pinnata, 12–15 cm longa et 13–15 cm lata, in sicco firma ; pinnae 3–6 ad apicem laminae versus vix decrescentes, imae 3–4-jugo-pinnulatae petiolis usque ad 1·5 cm longis instructae, ceterae pinnatisectae, sessiles, ambitu triangulares vel anguste

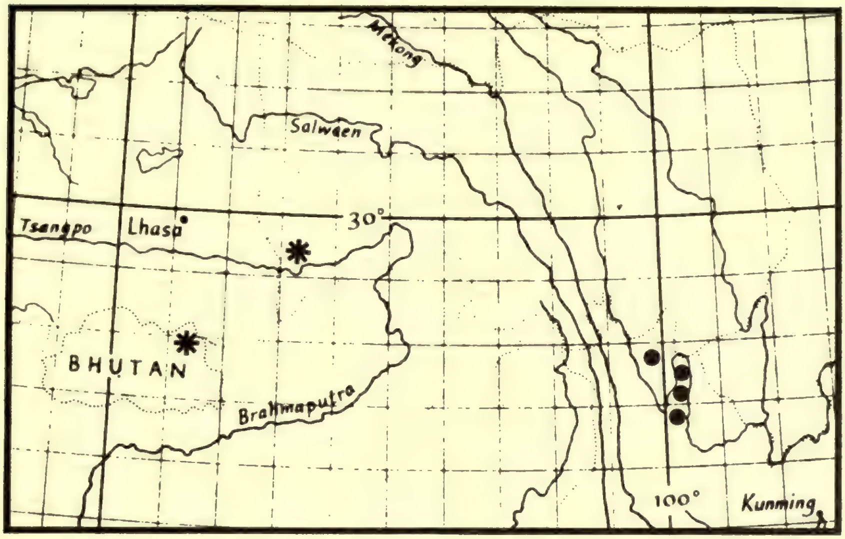

FIG. 3. Distribution of the genus *Haplosphaera* : ∗, *H. himalayensis* Ludlow ; ●, *H. phaea* Hand.-Mazz.

ovato-triangulares vel lanceolatae ; pinnulae 3–4, imae breviter petiolatae ceterae sessiles, profunde pinnatisectae, lobis mucronatis, acute dentatis ; *folia superiora* et fulcrantia (si obvia) basalia subconformia sed gradatim breviora, superiora sessilia. *Umbellae* 2–6, globosae vel subglobosae, 1·5–2·5 cm diametro, in statu immaturo ut videtur simplices in statu maturo compositae ; pedunculi 5–10 cm longi ; involucri bracteae nullae ; *umbellulae* 6–18-florae, pedicellis crassis, 2–3 mm longis ; involucelli bracteae 4–8, aciculatae, circiter 6 mm longae. *Sepala* inconspicua, triangulata. *Petala* late ovata, cucullata, obscure brunnea, apice acuta, circiter 1·5 mm longa et 1–1·25 mm lata. *Staminum* filamenta grisea, circiter 1 mm longa ; anterae virides, 0·75 mm longae. *Fructus* in statu immaturo 3 mm longus et 1·5 mm latus, latere visus obovatus ; mericarpia pentagona, 5-juga.

BHUTAN : Shingbe (Me La), 3900 m, 'flowers greenish brown, on open hillside ; whole plant very aromatic when crushed', 24 August 1949, *Ludlow, Sherriff & Hicks 21102*.

S.E. TIBET : Mira La, Nyang Chu, 3900 m 'up to 4 ft ; stony situations in clearings in abies forest ; ovary dark green, petals dull brown' 17 August 1938, *Ludlow, Sherriff & Taylor 6087* (holotype in Herb. Brit. Mus.).

This new species is placed in the genus *Haplosphaera* with some hesitation. When Handel-Mazzettii published this genus in 1921 for his Chinese plant *H. phaea*, he drew particular attention to the fact that it possessed simple umbels. Although at first glance the umbels of *H. himalayensis* appear to be simple, their compound nature becomes apparent as they mature. However, in the all-important characters of fruit and reproductive organs the two species are similar, whilst in general appearance, despite differences in foliage, they are obviously closely related. For the time being, therefore, it seems best to include this new Himalayan species in the genus *Haplosphaera*.

The brown petals make this plant easily recognizable among Himalayan Umbelliferae ; they contrast with the greenish-white filaments and dull green anthers. The fruit is olive green ; each mericarp is pentagonal, with the dorsal costa prominent.

CREMANTHODIUM (COMPOSITAE)

Cremanthodium bhutanicum Ludlow, sp. nov. (Plate 32A.)

Species *C. lineari* Maxim. affinis sed minor, ligulis apice obtusis tridentatis, non longe acutis.

Herba perennis, caulibus solitariis 8–25 cm altis, 1–2 mm diametro, striatis, superne arachnoideis ceterum glabris ; *caudex* petiolis angustis fibrosis erectis marcidis involucratus. *Folia* basalia 6–10, petiolata ; lamina linearis vel oblanceolato-linearis, 2–10 cm longa et 2–9 mm lata, glabra, integra, apice obtusa vel rotunda, basi angustissime cuneata, marginibus reflexis, supra pallide viridis subter glauca ; petiolus 1–5 cm longus, plus-minusve alatus, basi fibris brunneis numerosis circumdatus ; folia caulina 4–9, sessilia, linearia, apicem versus abrupte decrescentia, inferiora 2–3 cm, superiora 1–1·5 cm longa. *Capitula* in apice caulis solitaria, nutania, 2·5–3·5 cm diametro. *Involucri* squamae anguste lanceolatae ad lanceolatae, acutae, glabrae, laete vel obscure virides, saepe marginibus pallidis, 8–12 mm longae et 1·5–3 mm latae, venatione intus distincto extus obsoleto. *Bracteolae* 1 vel numerosae, graciles, basi capituli instructae. *Flores* radii feminei plerumque 12–13, omnes fertiles, tubo 1·5–2 mm longo ; ligula 1·25–2 cm longa et 2·5–5 mm lata, apice obtusa rare subacuta tridentata 4–7-nervia ; flores disci numerosi (30–40), hermaphroditi, omnes fertiles ; corolla 6–6·5 mm longa basi angustata, lobis acutis 0·75–1 mm longis. *Antherae* brunneae 2·5–3 mm longae. *Ovarium* glabrum ; stigmatis lobi fusci papillosi ; pappi squamae albae corollam superantes. *Achenia* fusca, glabra, ambitu oblonga vel anguste oblonga, 2–2·5 mm longa et 0·5–0·75 mm lata.

BHUTAN : Thampe la (27° 40′ N, 90° 16′ E), 4570 m, 'involucre olive green, ray florets pale yellow', 22 August 1949, *Ludlow, Sherriff & Hicks 17177* (holotype in Herb. Brit. Mus.). Worthang la (27° 57′ N, 90° 12′ E), 4250 m, 19 September 1949, *Ludlow, Sherriff & Hicks 17313*. Ju La, Mangde Chu Valley (27° 47′ N, 90° 34′ E), 440 m, 19 July 1949, *Ludlow, Sherriff & Hicks 16901*. Marlung, Tsampa (27° 56′ N, 90° 38′ E), 4570 m, 14 July 1949, *Ludlow, Sherriff & Hicks 19427*. Waitang, Tsampa (27° 57′ N, 90° 45′ E), 4700 m, 22 June 1949, *Ludlow, Sherriff & Hicks 19219*. Narim Thang (27° 57′ N, 91° 13′E), 4250 m, 26 July 1949, *Ludlow, Sherriff & Hicks 21355*. Narim Thang, Kang La, 4250 m, 18 August 1933, *Ludlow & Sherriff 471*. Narim Thang, Kurted, 4575 m, 1 August 1915, *R. E. Cooper 4279*. Singhi, Kurted, 4575 m, September 1915, *R. E. Cooper 4976*. Shingbe, Me La (27° 55′ N, 91° 33′ E), 4250 m, 13 June 1949, *Ludlow, Sherriff & Hicks 20728*. Shingbe, 4100 m, 2 September 1949, *Ludlow, Sherriff & Hicks 21141*.

ASSAM: Ze La (27° 31′ N, 92° 07′ E) 4575 m, 20 August 1938, *Kingdon-Ward 14123.*

The only *Cremanthodium* with linear leaves with which this new species might be confused is *C. lineare* Maxim. collected by Przewalski in Kansu in 1880. The shape and length of the ray florets readily serve to distinguish them. In *C. bhutanicum* the ray florets are from 1·25 to 2 cm long, with blunt, seldom subacute tips which are normally tridentate; in *C. lineare* the florets are from 2 to 3·5 cm long with long acute tips which are normally entire and only rarely notched.

In addition the Chinese plant is much the longer of the two with flowering stems up to 40 cm long bearing 9–14 cauline leaves, and with 12–14 radical leaves devoid of well-marked petioles. Moreover, in the abundant material of *C. bhutanicum* which is available the flowering stem is always solitary whereas in *C. lineare* there are frequently two stems on the same rootstock. So far as is known at present *C. bhutanicum* is confined to central and eastern Bhutan and extreme western Assam. It has not been recorded from Sikkim or south-eastern Tibet.

Cremanthodium campanulatum (Franch.) Diels in Notes R. bot. Gdn Edinb. 5 : 190 (1912).

Var. ***pinnatisectum*** Ludlow, var. nov. (Plate 32B.)

A typo (var. *campanulato*) foliis pinnatisectis distinguitur.

Burma–Tibet Frontier: Adung Valley (28° 20′ N, 97° 40′ E), 3950 m, 'scattered among low scrub on steep apline grass slopes. Flowers purple nodding. Involucral bracts deep purple covered with long bristly hairs. Ray florets 0. Leaves much divided with scattered hairs along the veins beneath. Flowers closely resemble those of 9861 but are much smaller. Leaves quite different', 27 July 1931, *Kingdon-Ward 9874* (holotype in Herb. Brit. Mus.). Adung Valley, 3960 m, 'two plants with sulphur yellow flowers otherwise like 9874 ; found on steep alpine turf slope amongst the very abundant no. (?)', 12 August 1931, *Kingdon-Ward 9930.*

The pinnatisect radical and cauline leaves of the above two gatherings contrast markedly with the reniform leaves of *C. campanulatum* but apart from this difference in leaf shape I can find no other character which is dissimilar. Since *C. campanulatum* itself varies considerably in size and colour it seems better to accord only varietal rank to these two gatherings from the Upper Irrawaddy.

SAUSSUREA (COMPOSITAE)

Saussurea neglecta Ludlow, sp. nov. (Plate 33A ; Text-fig. 4.)

Species affinis *S. deltiodeae* C. B. Clarke et *S. hypoleucae* Spreng. ex DC. ; ab ambabus statura humiliore usque ad 30 cm alta, foliis basi caulis aggregatis pagina superiore lanata vix scabrida discrepat.

Herba perennis, usque ad 30 cm alta, rhizomate lignoso conico crasso valido. *Caules* floriferi erecti 1–4 distincte striati lanuginosi in vivo rosei. *Folia basalia*

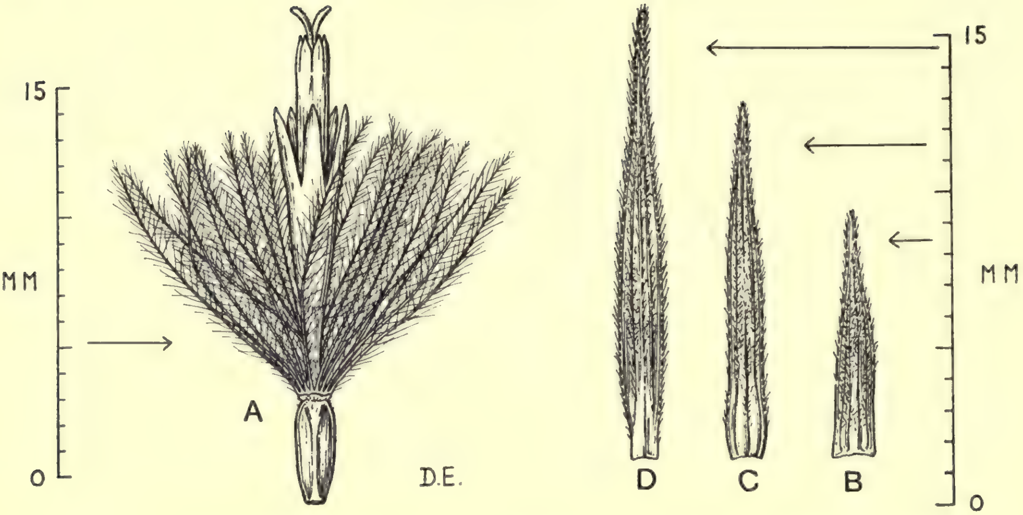

FIG. 4. *Saussurea neglecta* Ludlow ; A, floret ; B–D, involucral scales, B, outer, C, medium, D, inner (all from *Lowndes 1189*, holotype).

12–18 cm longa (petiolo incluso) 1·5–4 cm lata, lyrato-pinnatifida ambitu obovato-oblonga vel lanceolato-oblonga, supra lanuginoso-floccosa subtus dense albo-tomentosa, lobis lateralibus irregulariter sinuato-denticulatis, lobo terminale plerumque deltoideo ampliatoque, venatione indistincto ; *folia caulina* in parte inferiore caulis conferta, basalibus similia, in parte superiore dispersa et valde minora. *Capitula* nutantia, 2–3 cm diametro, in apicibus ramorum disposita, saepe cum 2–4 capitulis minoribus axillaribus. *Involucri phylla* 4–5-seriata, anguste lanceolata ad linearia, acuminata ; exteriora 6–8 mm longa, 0·75 mm lata, intus glabra et lucida, extus atro-pilosa et arachnoidea ; intermedia 8–11 mm longa et basi 1–1·25 mm lata ; interiora plerumque linearia, 12–13 mm longa, basi plus-minusve 1 mm lata, margine ciliata, apice fasciculo pilorum instructa. *Receptaculi* setae albae, aciculares, plusminusve 5 mm longae. *Flosculi* numerosi albi ad eburnei, *c.* 1 cm longi, corollae tubo quam limbo breviore. *Staminum* antherae 4–4·5 mm longae, caudis subulatis 2·5 mm longis instructis ; filamenta 0·8 mm longa. *Cypselae* (*achaenia*) obscure brunnea anguste oblonga, glabra, angulata, usque ad 3·5 mm longa, 1–5 mm lata. *Pappus* uniseriatus, albus, ad 1 cm longus, plumosus.

GARWHAL : Niti (30° 46′ N, 79° 52′ E), 3500 m, *Strachey & Winterbottom 9. Falconer* s.n. (K).

KUMAUN : Kutti Yangti Valley, Byans, 3000–3600 m, 30 July 1886, *Duthie 5712*. Parbhu Gori Valley, 3500 m, 14 August 1900, *Duthie 24539* (K).

NEPAL : Marsiandi Valley, 3500 m, 'river shingles, flowers white, turning buff, stems pinkish, leaves grey-green, silver on reverse', 13 July 1950, *Lowndes 1189* (holotype in Herb. Brit. Mus.). Tarap Valley, 4100 m, 'marginal flowers pinkish purple, central flowers woolly white', 17 July 1966, *Shrestha 5411*. Dolpo, Tarap,

4100 m, 'on stony slopes; flowers mauve, underside of leaf white', 18 July 1966, *Stainton 5554*.

This plant with nodding capitula and lyrate-pinnatifid leaves is allied to *S. deltoidea* C. B. Clarke – with which it has sometimes been confused – and *S. hypoleuca* Spreng. ex DC., but it is much smaller than either of these species, and does not exceed 30 cm in height. It may readily be distinguished from both by the cottony, not scabrid, nature of the upper surface of its leaves and by the flowering stems which spring from a rosette of basal leaves. It also resembles small scapose forms of *S. candicans* C. B. Clarke but the nodding capitula, tufted inner involucral segments and smooth achenes serve to distinguish it from that species.

The type-specimen (*Lowndes 1189*) was collected in Central Nepal at the extreme east (approx. 28° 35′ N 84° 12′ E,) of the known range of the species. The epithet *neglecta* refers to the first specimens having been collected more than a hundred years ago by Falconer, Strachey and Winterbottom.

SENECIO (COMPOSITAE)

Senecio kongboensis Ludlow, sp. nov. (Plate 33B; Text-fig. 5.)

Herba perennis pumila 2–5 cm alta, caulibus e rhizomate fibroso erectis ramosis arachnoideis. *Folia* congesta, infima breve petiolata ad 1 cm longa, alata, reliqua sessilia; lamina lanceolata vel lineari-lanceolata, usque ad 3 cm longa, 0·6 cm lata, supra glabra vel glanduloso-pilosa, subtus albo-arachnoidea, marginibus reflexis irregulariter denticulatis, nerviis secundariis non prominulis percursa. *Capitula* breve pedunculata vel subsessilia aliquot (5–25) in inflorescentia dense corymbiformi 2–4 cm lata disposita. *Involucri* squamae 12–13 lineares vel lineari-lanceolatae 6–7 mm longae, 0·5–1 mm latae glabrae acutae apice marginibusque obscure purpureae ceterum virides. *Bracteae* 5–6 aciculatae 4–5 mm longae. *Flores radii*

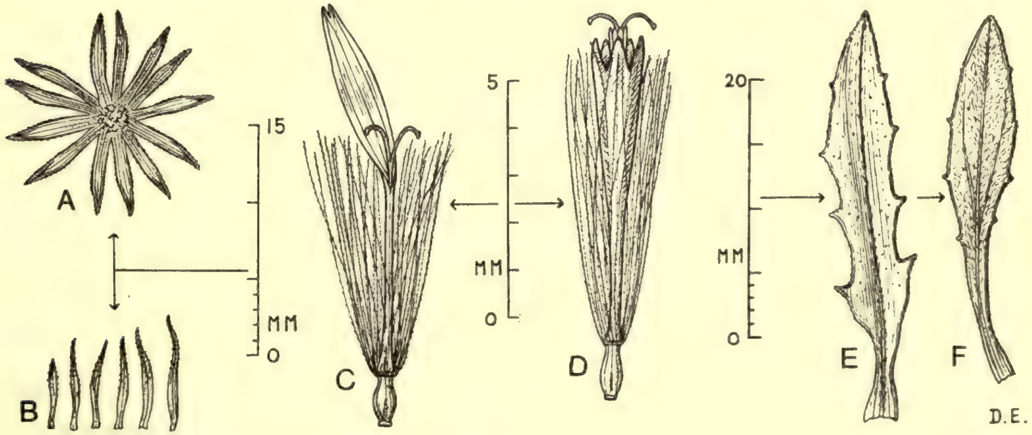

FIG. 5. *Senecio kongboensis* Ludlow; A, involucre; B, bracts; C, ray floret; D, disc floret; E, F, basal leaves (all from *L S & E 14432*, holotype).

feminei ligulati plerumque 6–10 lutei, tubo gracilimo 3–4 mm longo, limbo plusminusve 3 mm longo 0·5 mm lato, 1–2 (raro 3) nerves; pappi setae gracilimae minute scabridae 5 mm longae. *Flores disci* 12–25 hermaphroditi omnes fertiles, tubo corollae cylindrico 5 mm longo, basi 0·25 mm lato, apicem versus 1 mm diametro, lobis usque ad 0·75 mm longis nigrescentibus. *Stamina* 5; antherae *c.* 1·5 mm longae, 0·15 mm latae; filamenta gracilima 3 mm longa. *Cypselae* (*achaenia*) glabrae in statu immaturo 1·5 mm longae 0·75 latae.

S.E. TIBET: Budi Tsepo La (29° 27′ N, 94° 57′ E), 4000 m, 22 August 1947, 'involucre green tipped darker at apex, florets yellow, in wet scree', *Ludlow, Sherriff & Elliot 14432* (holotype in Herb. Brit. Mus.).

This dwarf species is closely related to *S. bracteolatus* Hook. f. and *S. thianschanicus* Regel & Schmalh. Its small capitula, however, are most nearly matched by those of *S. kawaguchii* Kitamura (in *Acta phytotax. geobot. Kyoto* **15**: 75 (1953)), of which *S. drummondii* Babu & S.N. Biswas in *J. Jap. Bot.* **46**: 23, fig. 1 (1971) is a synonym; both were based on specimens collected near Lhasa. It differs from all these species in the very short 1–3 veined ligules of the ray florets and the black-tipped corolla lobes of the disc florets, and more especially by its dwarf stature and congested foliage and inflorescence.

DIAPENSIA (DIAPENSIACEAE)

Diapensia wardii W. E. Evans in Notes R. bot. Gdn Edinb. 15: 233 (1927). (Plate 34B; Text-fig. 6D–F.)

Diapensia wardii W. E. Evans was described from a fruiting gathering obtained by Kingdon-Ward on the Doshong La, south-eastern Tibet, in October 1924. In his 'A revision of the genus Diapensia' Evans (loc. cit.) remarked: 'Though the flowers are at present unknown, it may be predicted with confidence that, when found, they will prove to be practically sessile and to possess, normally, simple staminodes, as in the case of *D. himalaica*, Hook. f. et Thoms. and *D. purpurea*, Diels, the only other members of the genus inhabiting the same geographical area. The peduncles, it may be safely assumed, do not elongate until after fertilization of the flowers has taken place. They do not seem to differ, either in this respect or in their colour, from what is usual throughout the Section *Himalaicae*.'

This prediction has proved incorrect. Flowering plants obtained in south-eastern Tibet by Ludlow and Sherriff in 1936, and by Ludlow, Sherriff and Taylor, from the type locality, in 1938, and by Kingdon-Ward in Assam, also in 1938, have peduncles just as well developed as they are in *D. lapponica* L. In the field notes accompanying Kingdon-Ward's gathering from Assam, the flowers are said to be 'nodding on inch long stalks'. In *Ludlow & Sherriff 2346* (Plate 34B) the flowers are also nodding though the collectors do not mention this in their notes.

The stamens and staminodes in *D. wardii* are very distinctive (Fig. 6D–F). The loculi of the anthers, it will be observed, are divaricate and are placed end to end, almost in a straight line. In *D. himalaica* (Plate 34A; Fig. 6A–C) they are merely divergent, and in *D. purpurea* they may be divergent or parallel (l.c. 217, Fig. 1).

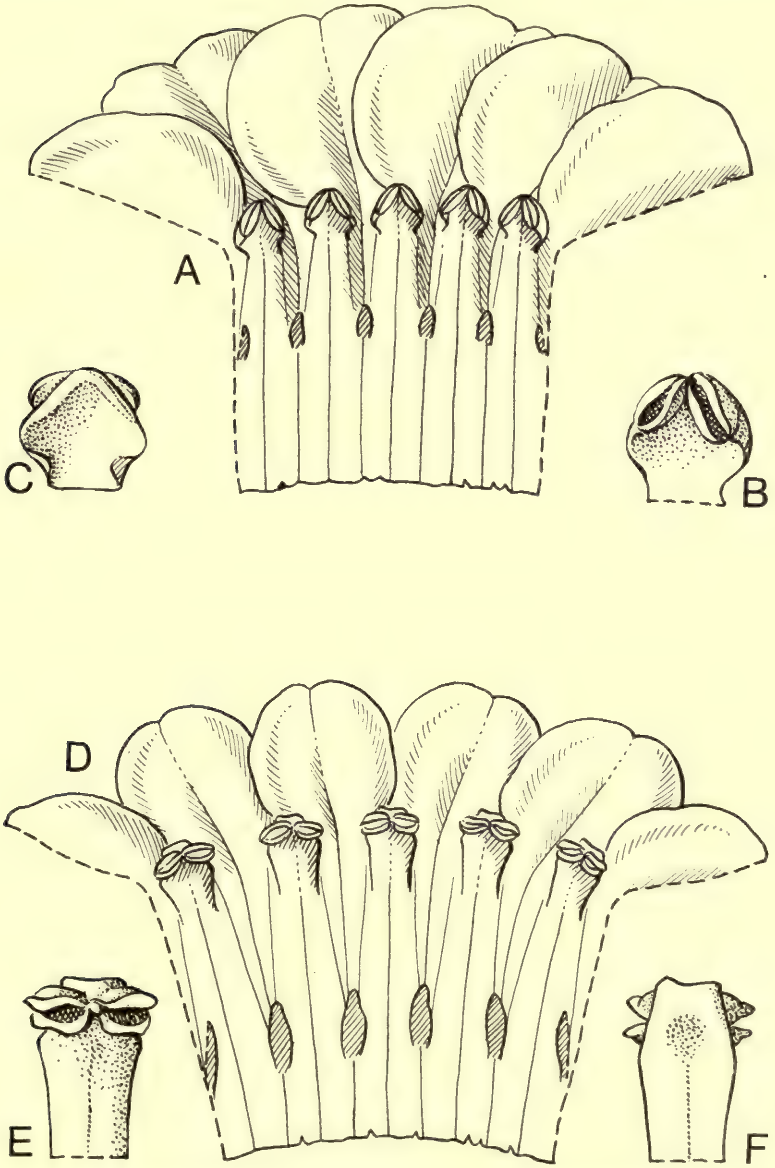

FIG. 6. *Diapensia himalaica* Hook. f. & Thoms. ; A, corolla opened out, × 4½ ; B, stamen, anterior view ; C, stamen, posterior view (all from *L S & T 4754*), × 4½. *D. wardii* W. E. Evans ; D, corolla opened out, × 4½ ; E, stamen, anterior view, × 9 ; F, stamen, posterior view, × 9 (all from *L S & T 5227*).

The staminodes in *D. wardii* are well developed, and are attached below the middle of the corolla tube and not above it as in *D. himalaica* and *D. purpurea*. In a fruiting gathering, *Ludlow, Sherriff & Taylor 6246*, made on 15 October 1938, the peduncles vary in length from 8 to 12 cm, measurements considerably in excess of those previously recorded.

Evans divided the four known species of the genus into two groups or sections based on their structural and distributional peculiarities as follows :—

'SECTIO 1. *Lapponicae.* Flores sub anthesi normaliter pedunculis 1–1·5 cm longis suffulti ; staminodia nulla. Species unica (*D. lapponica* Linn.) Americae borealis, Europae borealis, Asiae borealis et Ins. Japoniae incola.

SECTIO 2. *Himalaica.* Flores sub anthesi subsessiles, pedunculi tantum fructu maturescente elongantes ; staminodia normaliter 5 parva simplicia corollae tubum medium versus affixa, in speciminibus nonnullis numero reducta vel O. Species tres, montibus sino-himalaicis circumscripti.'

In Section 1, he placed the circumpolar species *D. lapponica* L. ; the three remaining species, *D. himalaica* Hook. f. & Thoms., *D. purpurea* Diels and *D. wardii* W. E. Evans, he placed in Section 2, assuming that the flowers of the last-named species when found would be practically sessile. The flowers of *D. wardii*, however, have proved to be pedunculate at the time of flowering and hence the species should be included in section *Lapponicae.* But *D. wardii* also possesses staminodes, a character that places it in section *Himalaicae.* It thus has characters justifying its inclusion in both sections. In these circumstances, since the genus consists of only four known species, it seems unnecessary to divide this into sections. Evans's key to the species, which separates *D. wardii* from the others by its larger leaves, is, however, not affected by this. Since no account of the floral organs of *D. wardii* has so far been published, a description of these is herewith appended together with a list of gatherings made subsequent to the original discovery of the species in 1924 :

Flowers solitary, nodding, on crimson peduncles 1–3 cm long, 1 mm wide, at the time of flowering. *Bracts* 2 or 3, 5–6 mm long, 2–2·5 mm wide. *Calyx* 5-partite ; sepals glabrous, crimson, obovate or narrowly obovate, obtuse, 5–6 mm long, 2·5–3·5 mm wide. *Corolla* rich rose or wine red ; lobes 5, orbicular or rounded, 6–7 mm long, 5–6 mm wide ; tube 7·5–9 mm long, 4–5 mm in diameter. *Stamens* alternating with corolla lobes, inserted at throat of corolla tube ; filaments 1·75–2·25 mm long, 1·25–1·40 mm wide ; anthers divaricate ; staminodes 5, conical, 2 mm long, 0·5–0·75 mm wide, alternating with stamens, attached below middle of corolla tube. *Ovary* globose, glabrous ; style crimson, filiform 5–8 mm long, 0·5 mm wide, reaching the throat, occasionally extruded ; stigma faintly tri-lobed. *Capsule* globular, 2·5–3 mm long, 2·5–3 mm wide, trilocular ; seeds minute, numerous.

ASSAM : Poshing La (27° 32′ N, 92° 25′ E), 3500 m, 'A creeping plant forming mats, but not cushions like *D. himalaica*, on mossy rocks. Flowers rose pink, nodding on inch-long stalks, reaching 2 inches in fruit', 20 July 1938, *Kingdon-Ward 13950.*

S.E. TIBET : Karutura, Chayul Chu (28° 20′ N, 93° 02′ E), 4000 m, 'Corolla very bright wine red, filaments the same, anthers greenish, style bright rose, stigma green. In clumps growing under rhododendrons besides rocks in moss', 12 July 1936, *Ludlow & Sherriff 2346*. Bimbi La, Tsari District (28° 44′ N, 93° 10′ E), 3600 m, 'On steep scree', 15 October 1938, *Ludlow, Sherriff & Taylor 6346*. Doshong La (29° 29′ N, 94° 59′ E), 4100 m, 'Grows through moss in swamp either in open or under dwarf rhododendrons, corolla rich rose-pink (also broad flattened filaments), anthers, separated at apex of filaments, dull yellow. Peduncles and calyces light crimson', 13 July 1938, *Ludlow, Sherriff & Taylor 5227, 5227a.*

ANDROSACE (PRIMULACEAE)

Androsace nortonii Ludlow, sp. nov. (Plate 35 ; Text-fig. 7.)

Planta ex affinitate *A. limprichtii* Pax et Hoffm. a qua habitu minore, scapis pedicellisque pergracilibus, planta tota pilis albidis obtectis recedit.

Herba perennis caespitosa stolonifera, stolonibus glabrescentibus internodiis 0·5–2·5 cm longis cortice brunneo obtectis. *Folia* rosulata trimorpha sericeovillosa, pilis albidis usque ad 2·5 mm longis ; *folia externa* anguste elliptica, plusminusve 5 mm longa, 1·5 mm lata, brunnea ; *folia intermedia* lingulata ad lingulato-spathulata, 4–7·5 mm longa 0·75–2 mm lata, viridia, basi hyalina, apice obtusa ; *folia interna* petiolata ; lamina elliptica, 3·5–6 mm longa, 2–3 mm lata, viridis, apice obtusa ; petiolus 3·5–6 mm longus. *Scapus* 2–6 cm longus, 0·3–0·5 mm diametro, gracilimus. *Flores* in umbellis 2–6-floris terminalibus dispositi ; pedicelli 2–9 mm longi, filiformes pilosi. *Bracteae* lineares, 2–3·5 mm longae, villosae. *Calyx* cupularis, plusminusve 3 mm longus, dense pilosus, 5-lobatus, ad medium fissus, lobis anguste ovatis, trinerviis, apicem versus purpureis. *Corolla* rosea, 7–9 mm diametro, tubo 2·5–2·75 mm longo, 1·5 mm diametro, limbo profunde fisso, lobis late obovatis. *Stamina* tubo corollae inserta et in hoc inclusa ; antherae oblongae, 0·5 mm longae ; filamenta 0·3–0·4 mm longa. *Ovarium* plusminusve 1 mm longum, 1·4 mm diametro ; stylus usque ad 0·75 mm longus. *Capsula* ignota.

NEPAL : Chhairogaon, north of Tukucha, 3500 m, 'on open hillside ; flowers pink', 31 May 1954, *Stainton, Sykes & Williams 832*. Thinigaon, Muktinath Himal, 4500 m, 'open stony slopes, flowers pink, leaves hairy', 23 June 1954, *Stainton, Sykes & Williams 1362* (holotype in Herb. Brit. Mus.). Jargeng Khola, 4250 m, 'flowers rose-pink, darker eye, sparingly on glacial flats on turf, and on open hillsides, often in shelter of dwarf shrubs', 21 June 1950, *Lowndes 1030*. Jargeng Khola, 4500 m, 'in coarse turf on open hillside ; leaves and rosettes silvery', 6 July 1950, *Lowndes 1140*. Shiar Khola, 4000 m, 28 May 1953, *Gardner 622*. Khola Kharka, 4100 m, 17 July 1949, *Polunin 1078*. Arun Valley, Barun Khola, north of Num, 4000 m, 12 June 1956, *Stainton 636*.

TIBET : Chog La, Karma Valley, 4500 m, Mt Everest Exped. 1922, 'stony soil', *Norton 247*.

A fragment of this attractive little plant was collected by Major E. F. Norton in the Karma Valley during the Mt Everest Expedition of 1922. When Handel-Mazzetti

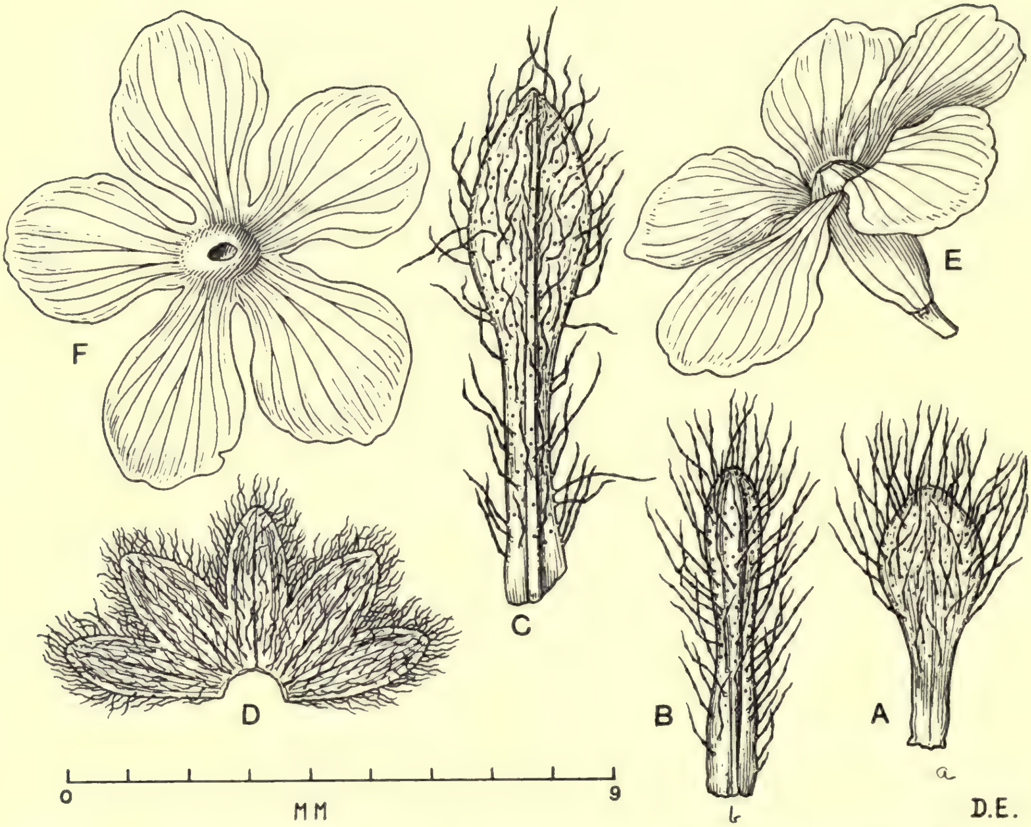

FIG. 7. *Androsace nortonii* Ludlow ; A, outer leaf ; B, median leaf ; C, inner leaf ; D, calyx opened out ; E, corolla, side view ; F, corolla from above (all from *S S & W 1362*, holotype).

examined it in 1927 he placed it in the series *Hookeriana* with *A. limprichtii* Pax et Hoffm. as its nearest relative. This seems to be its true position, but it differs from *A. limprichtii* in several particulars, the chief of which are its dwarf habit, its slender, almost filiform, scapes and pedicels, and the profuse white hairs covering the entire plant. From *A. villosa* L., to which it bears a superficial resemblance, it is at once distinguished by its trimorphic leaves.

CORYDALIS (PAPAVERACEAE)

[Mr Ludlow's notes on the following two species, having been inadvertently left apart from his other material, came to light after the paper 'New Himalayan and Tibetan Species of *Corydalis* (Papaveraceae)' by Ludlow and Stearn in *Bull. Br. Mus. nat. Hist.* (Bot.) **5** (2) (issued 14 February 1975) had been printed. *Corydalis brevicalcarata* Ludlow is accordingly to be added to the list of endemic Nepal species on p. 48 of that paper.]

Corydalis brevicalcarata Ludlow, sp. nov. (Plate 36; Text-fig. 8.)

Herba perennis, caespitosa, glabra, 10–20 cm alta. *Radix palaris* simplex, ad 9 cm vel ultra longa. *Caules* numerosi, ad 20 cm longi, e basi ramosi. *Folia basalia* 3–5 cm longa, 1–1·5 cm lata, ambitu oblongo, pinnatim 3–5 jugata; pinnae subaequales, oppositae vel fere oppositae, infimae breviter petiolulatae, ceterae subsessiles vel sessiles, 6–8 mm longae, 5–6 mm latae, trilobatae, lobis iterum irregulariter trilobatis obtusis. *Folia caulina* basalibus similia. *Inflorescentiae* terminales et laterales, racemosae, 6–12-florae; pedicelli graciles, ad 9 mm longi. *Bracteae* infimae interdum trilobatae, ceterae lanceolatae, integrae, *c.* 3 mm longae. *Flores* parvi, ascendentes, lutei. *Sepala* ovata vel oblonga, leviter dentata, *c.* 1·5 mm longa. *Petalum posticum* 8–9 mm longum (calcari incluso), ecristatum; calcar conicum, 2–2·5 mm longum; *petalum anticum* 6–7 mm longum, ecristatum; *petala interiora* 6·5 mm longa (unguiculo 3 mm longo incluso). *Stamina* (synandria) 5 mm longa. *Ovarium* obovatum; *stylus* gracilis, 2·5 mm longus; *stigma* profunde fissum, V-forme, sine cornibus posterioribus.

NEPAL: Bhurchula Lekh, near Jumla (29° 14′ N, 82° 07′ E), 3700 m, 'Growing in rock ledges over which water flows. Perianth yellow', 14 July 1952, *Polunin, Sykes & Williams 4684* (holotype in Herb. Mus. Brit.).

The small pinnate leaves with trilobed pinnae and the small yellow flowers, 8–9 mm long, with short tapering spurs only 2–2·5 mm long, whence the specific epithet, are the most obvious characters of this elegant little chasmophyte. An important character visible only on dissection is the V-shaped cleft of the stigma. The species must be very local in distribution as, despite the many wide-ranging expeditions made in Nepal, it seems to have been collected only once.

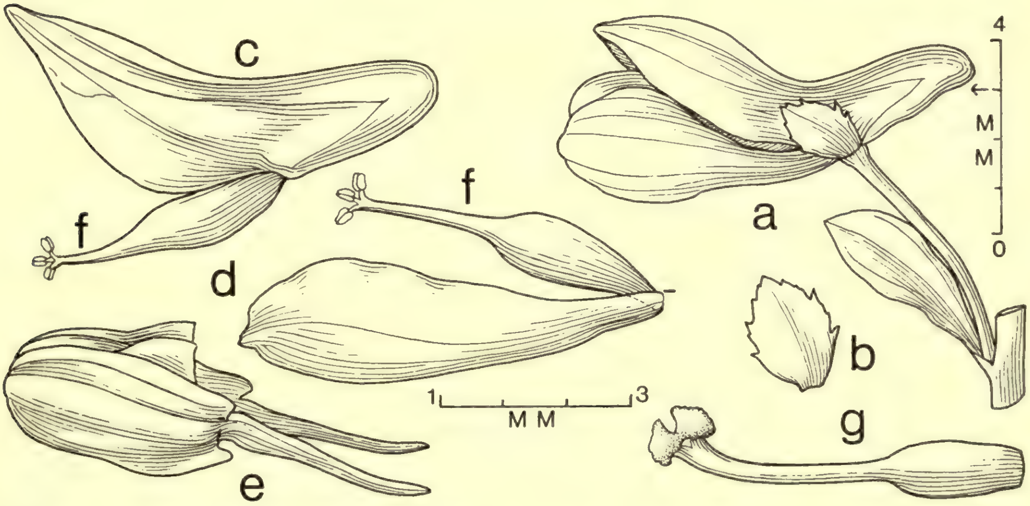

FIG. 8. *Corydalis brevicalcarata* Ludlow; a, flower with bract; b, sepal; c, posticous petal; d, anticous petals; e, inner petals; f, phalange with anthers; g, gynoecium (*P S & W 4684*).

Corydalis sherriffii Ludlow, sp. nov. (Plate 37; Text-fig. 9.)

Herba perennis, erecta, subglabra, gracilis, 15–25 cm alta. *Caudex* brevis, praemorsus, reliquiis paucis foliorum marcidis ad 1 cm longis coronatus, radices filiformes emittens. *Caules* simplices, ad 25 cm alti. *Folia basalia* numerosa, longipetiolata, caule florifero multo breviora, 10–18 cm longa (petiolo 7–15 cm longo incluso); lamina pinnata, pinnis alternis vel oppositis trisectis (mediano interdum profunde bisecta) petiolulatis; pinnulae lineares vel anguste lanceolatae, 1–2 cm longae, 2–5 mm latae, acutae, inconspicue trinerviae. *Folia caulina* 2, distantia, infimum brevipetiolata, superum subsessile vel sessile; lamina irregulatim pinnata, pinnis bisectis vel trisectis, pinnulis eis foliorum basalium similibus sed minoribus. *Inflorescentia* terminalis, racemosa, congesta, 6–12-flora; pedicelli graciles, ad 1 cm longi. *Bracteae* pinnatifidae, 0·6–1·5 cm longae. *Flores* ascendentes, malvini praeter petala interiora alba. *Sepala* decidua, semi-lunaria, margine lacerata, 1 mm longa. *Petalum posticum* 17 mm longum (calcari incluso), cristatum; calcar rectum, 7·5 mm longum, glande nectarifera *c.* 3·5 mm longa; *petalum anticum* 10 mm longum, cristatum; *petala interiora* 8 mm longa (unguiculo 3 mm longo incluso). *Stylus* elongatus, 4 mm longus; *stigma* rectangulare, papillis anterioribus 4, cornibus prominentibus 2.

TIBET: Kulu Phu Chu, near Paka (29° 15′ N, 94° 25′ E), 4500 m, 'Inner petals white, outer petals dark mauve. On open grassy ledges, steep rocky hillside', 27 July 1938, *Ludlow, Sherriff & Taylor 5969* (holotype in Herb. Mus. Brit.).

This species of south-eastern Tibet dedicated to George Sherriff (1898–1967) resembles in general appearance *C. rheinbabeniana* Fedde, described in 1924 from material collected by Harry Smith in Szechwan, but it is less robust with smaller mauve straight flowers, not orange and sigmoid as in *C. rheinbabeniana*, forming a small congested terminal raceme, and it has a fibrous and not tuberous root-system.

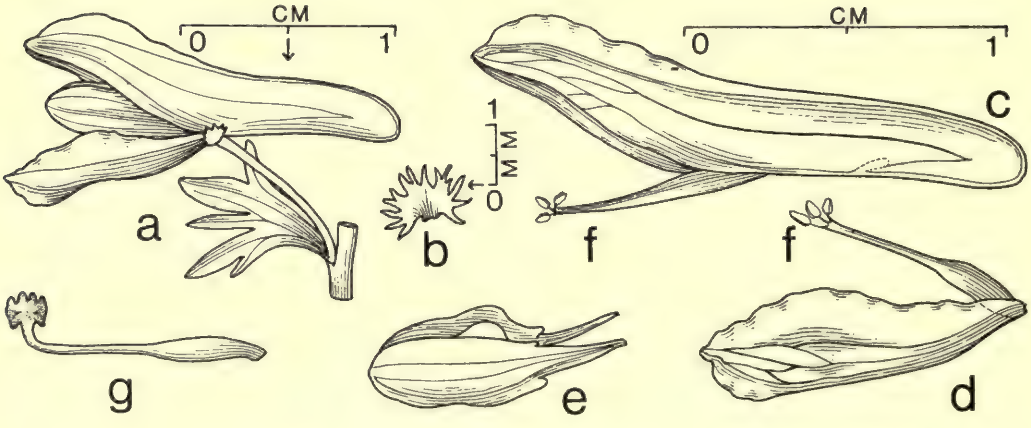

FIG. 9. *Corydalis sherriffii* Ludlow; a, flower with bract; b, sepal; c, posticous petal; d, anticous petal; e, inner petals; f, phalange with anthers; g, gynoecium (*L S & T 5969*).

F. Ludlow, O.B.E., M.A.
(*deceased* 1972)
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Department of Botany
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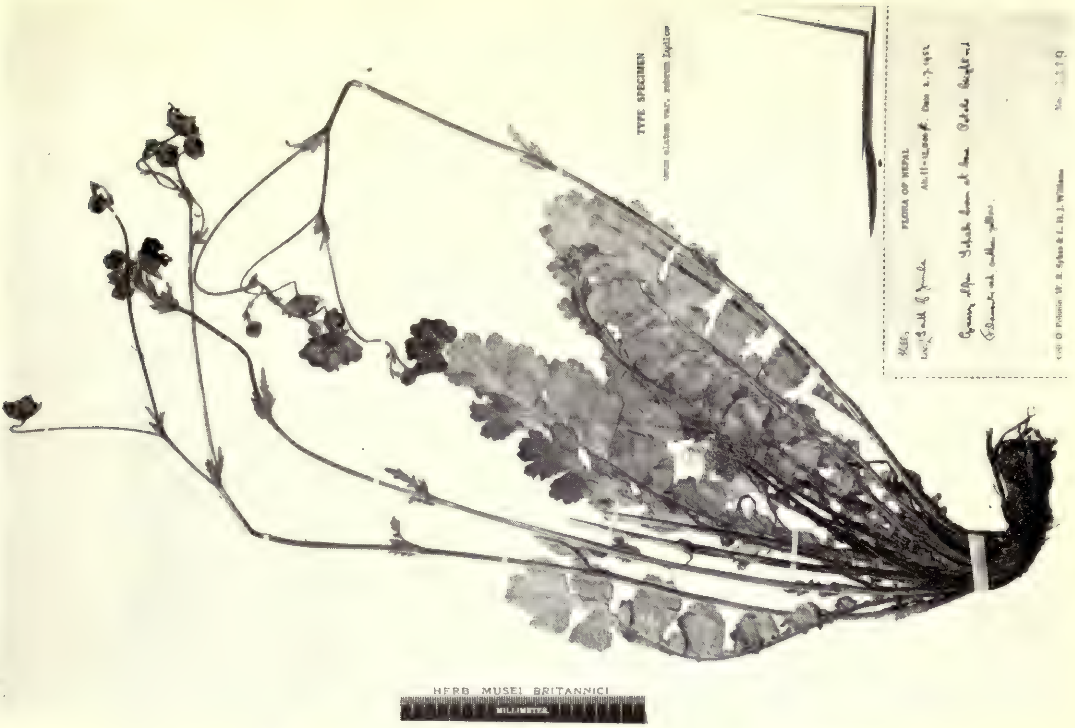
PLATE 30

A (left) *Geum macrosepalum* Ludlow (*Ludlow, Sherriff & Hicks 19171* ; holotype).
B (right) *Geum elatum* var. *rubrum* Ludlow (*Polunin, Sykes & Williams 4419* ; holotype).

PLATE 30


TYPE SPECIMEN
Geum elatum var. rubrum Ludlow
FLORA OF NEPAL
Coll. O. Polunin W. R. Sykes & L. H. J. Williams
HERB. MUSEI BRITANNICI
MILLIMETER

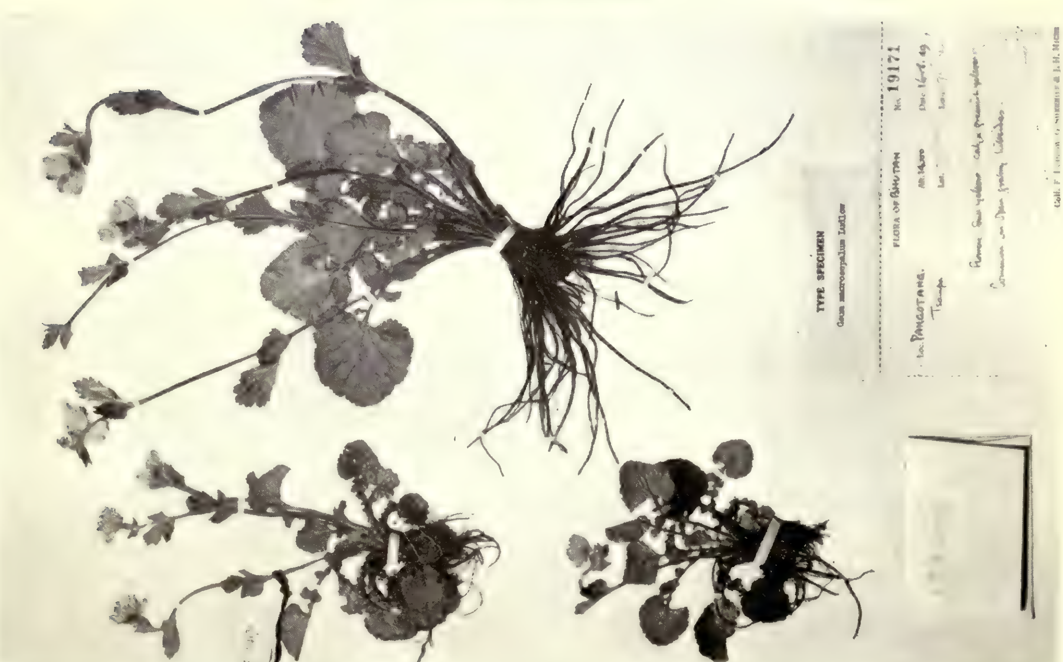

TYPE SPECIMEN
Geum macrosepalum Ludlow
FLORA OF BHUTAN
No. 19171
Loc. Pangotang.
Tsampa

PLATE 31

Haplosphaera himalayensis Ludlow (*Ludlow, Sherriff & Taylor 6087* ; holotype).

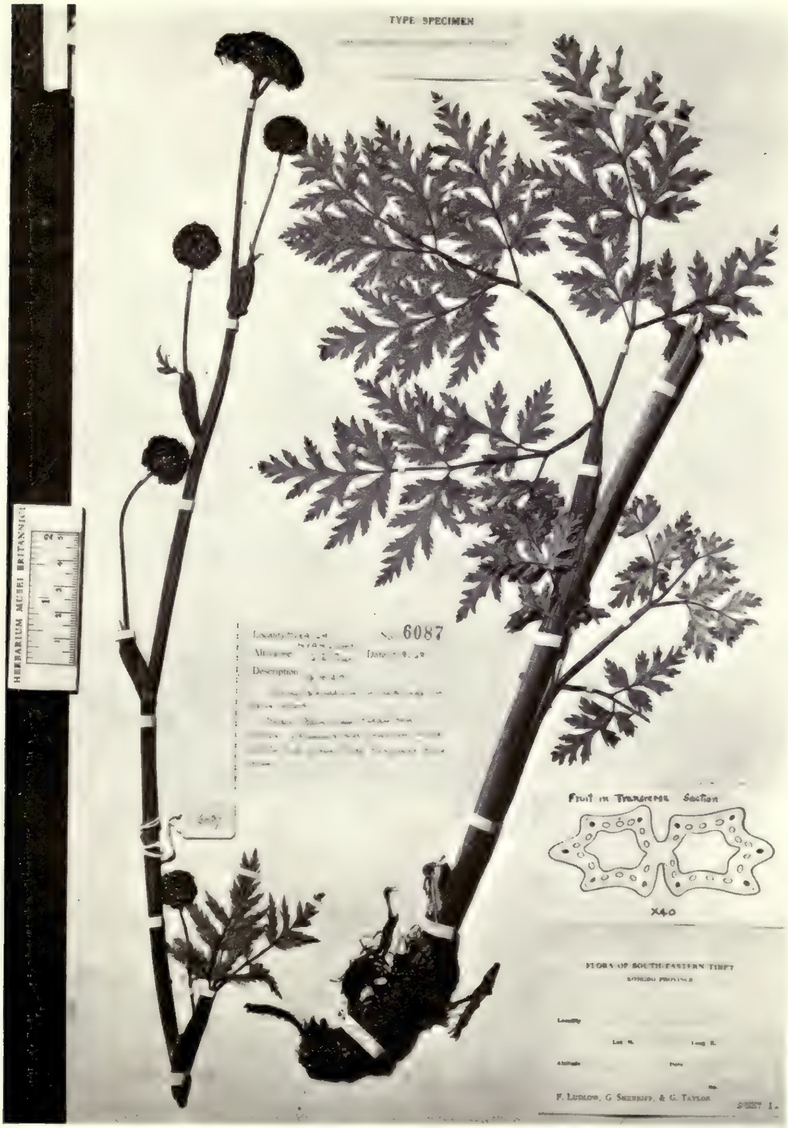
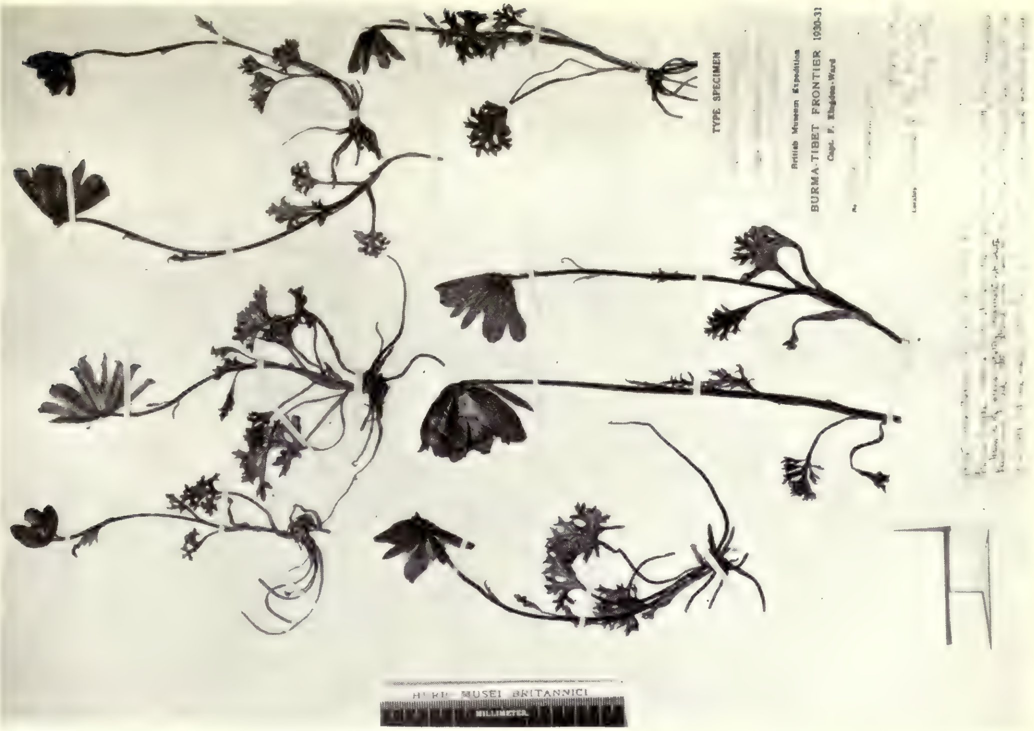

TYPE SPECIMEN
HERBARIUM MUSEI BRITANNICI
6087
Locality
Altitude
Date
Description
Fruit in Transverse Section
X40
FLORA OF SOUTH-EASTERN TIBET
Locality
Lat. N.
Long. E.
Altitude
Date
No.
F. Ludlow, G. Sherriff, & G. Taylor
SHEET 1.

PLATE 32

A (left) *Cremanthodium bhutanicum* Ludlow (*Ludlow, Sherriff & Hicks 17177*; holotype).

B (right) *Cremanthodium campanulatum* var. *pinnatisectum* Ludlow (*Kingdon-Ward 9874*; holotype).


TYPE SPECIMEN
British Museum Expedition
BURMA-TIBET FRONTIER 1930-31
Capt. F. Kingdon-Ward
HERB. MUSEI BRITANNICI
MILLIMETER

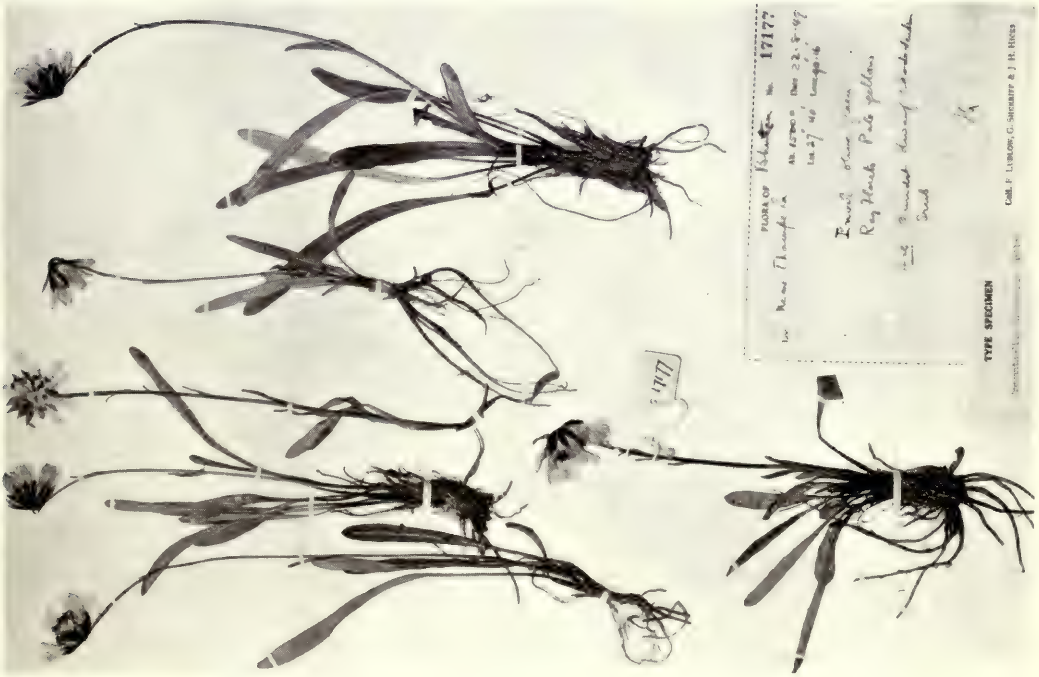
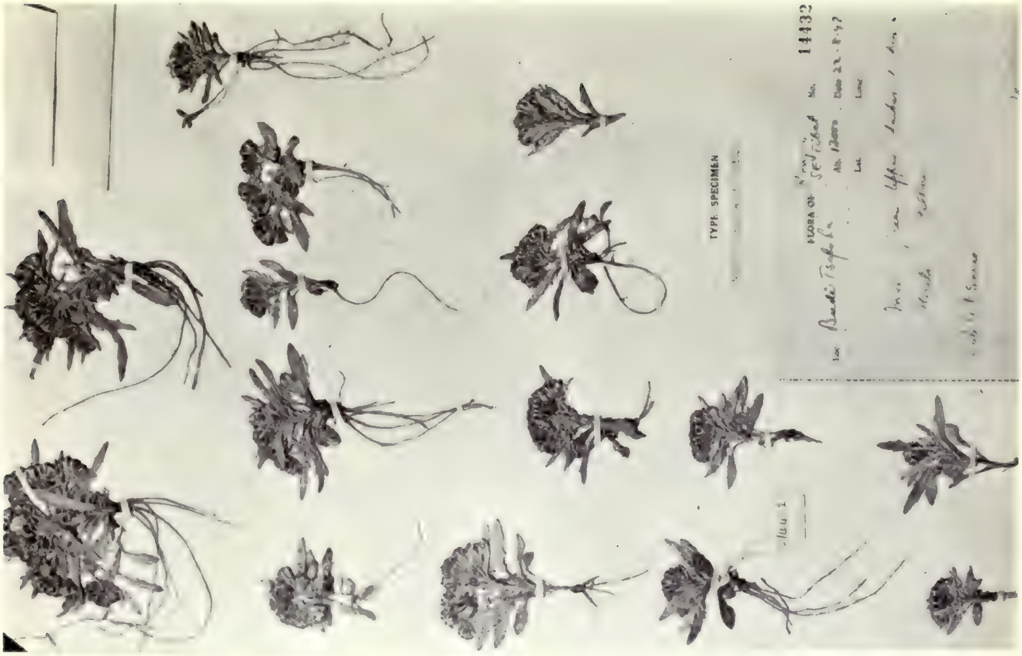

FLORA OF Bhutan No. 17177
TYPE SPECIMEN
Coll. F. LUDLOW, G. SHERRIFF & J. H. HICKS
17177

PLATE 33

A (left) *Saussurea neglecta* Ludlow (*Lowndes 1189* ; holotype).
B (right) *Senecio kongboensis* Ludlow (*Ludlow, Sherriff & Elliott 14432* ; holotype).


TYPE SPECIMEN
FLORA OF SE Tibet
14432

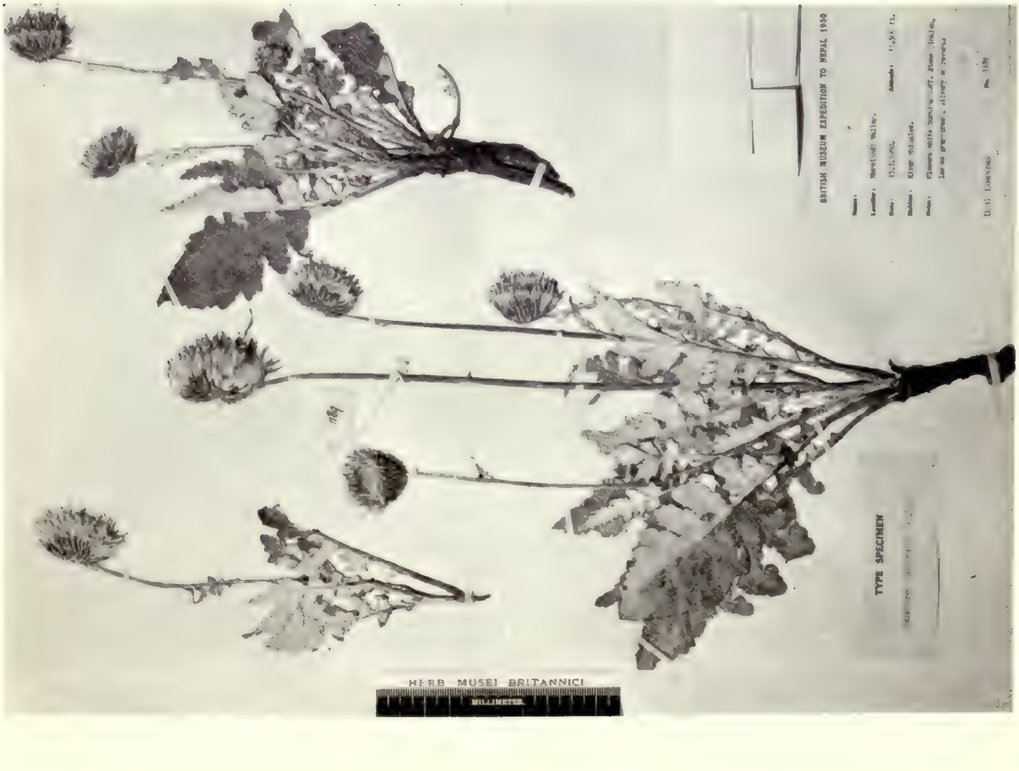
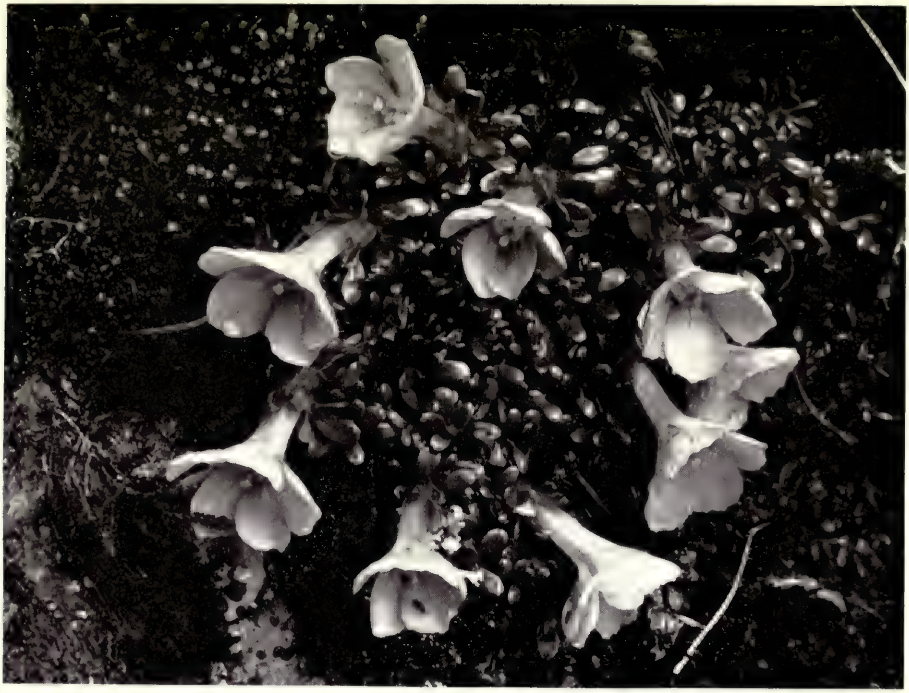

BRITISH MUSEUM EXPEDITION TO NEPAL 1950
TYPE SPECIMEN
HERB MUSEI BRITANNICI
MILLIMETER

PLATE 34

A (above) *Diapensia himalaica* Hook, f. & Thoms. (*Ludlow, Sherriff & Hicks 20629*).
B (below) *Diapensia wardii* W. E. Evans (*Ludlow & Sherriff 2346*).



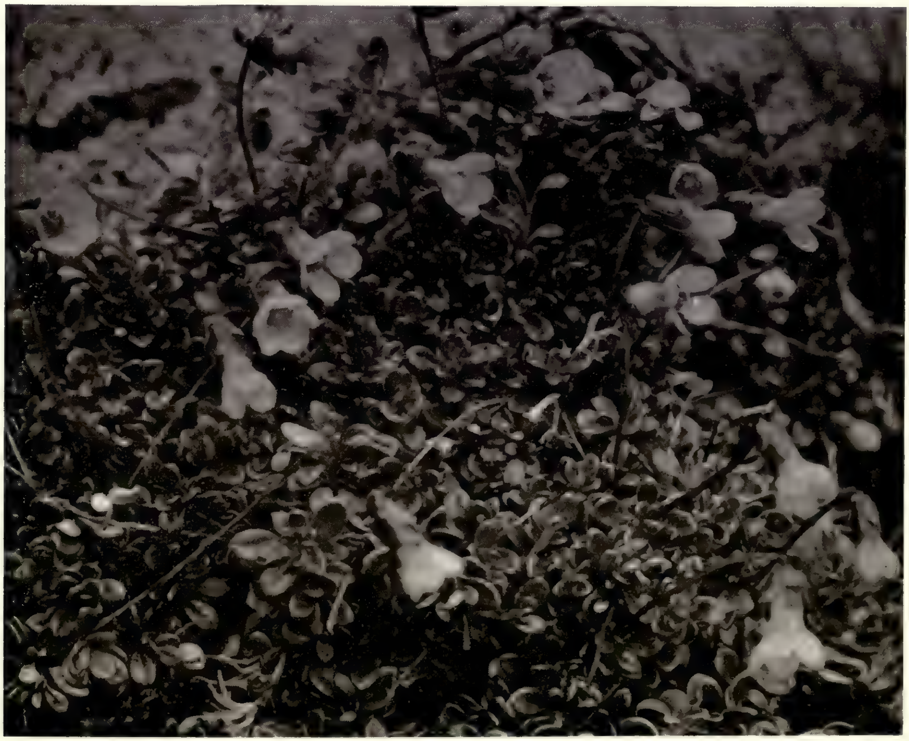


PLATE 35

Androsace nortonii Ludlow (*Stainton, Sykes & Williams 1362* ; holotype).

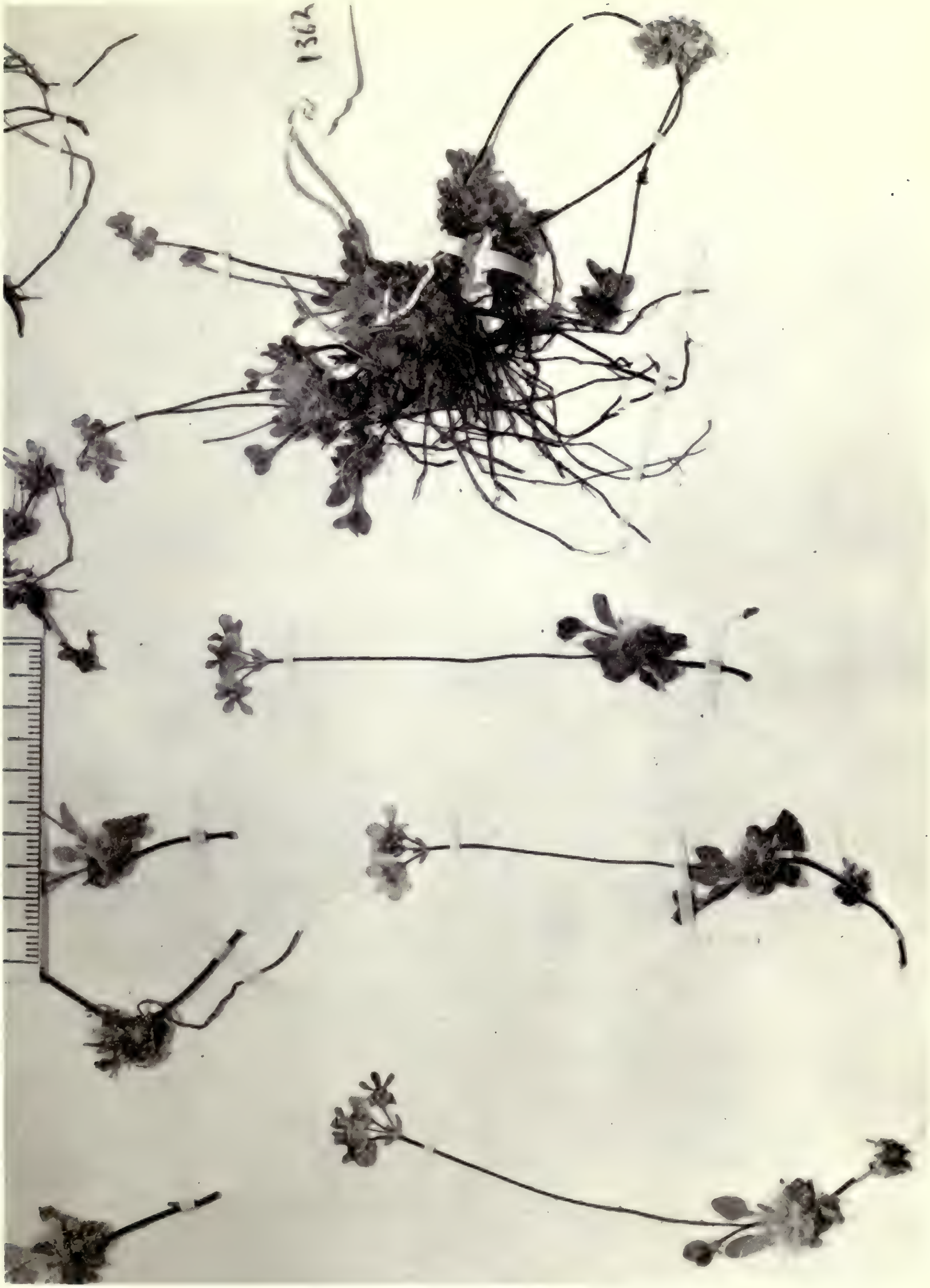
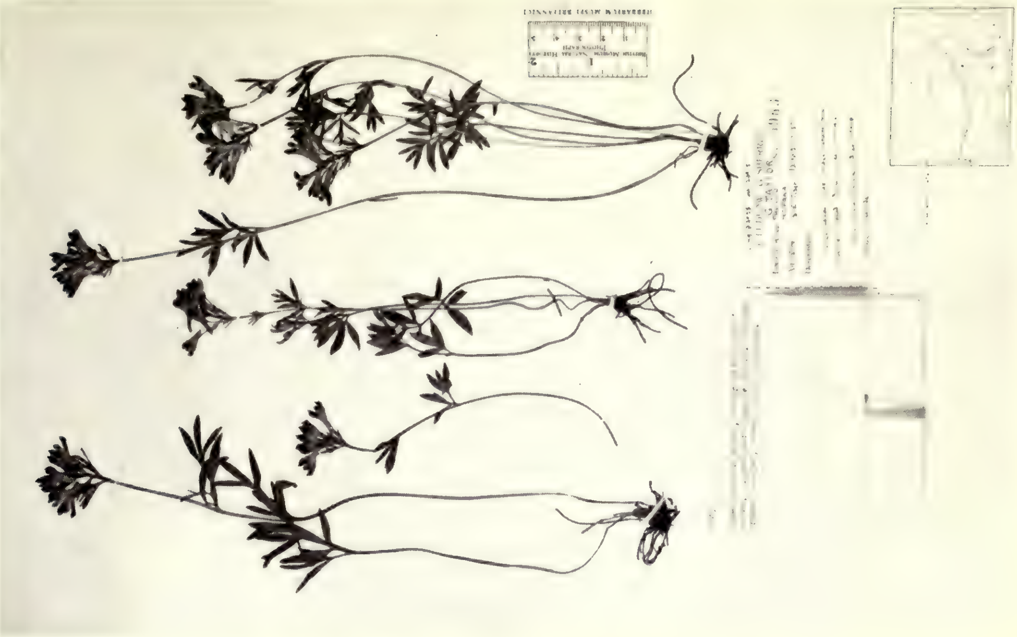
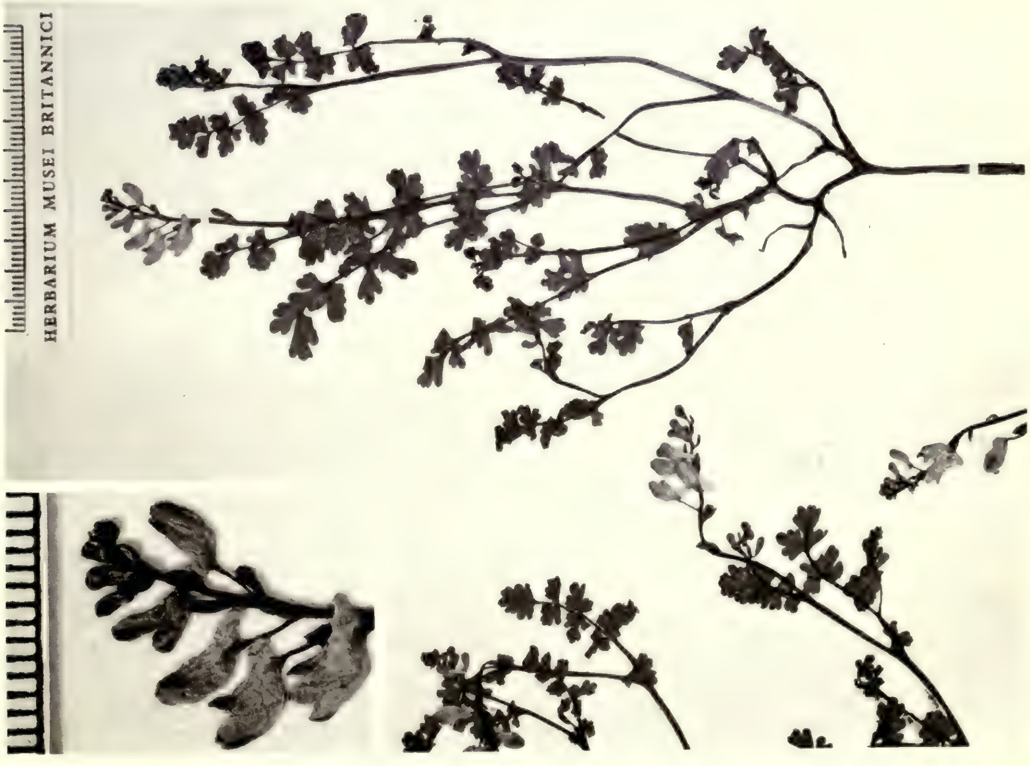

1362

PLATE 36

A (left) *Corydalis brevicalcarata* (*Polunin, Sykes & Williams 4684* ; holotype).

B (right) *Corydalis sherriffii* Ludlow (*Ludlow, Sherriff & Taylor 5969* ; holotype).

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BM. B

STUDIES IN THE GENUS *HYPERICUM* L. (GUTTIFERAE). 1. INFRAGENERIC CLASSIFICATION

N. K. B. ROBSON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
BOTANY Vol. 5 No. 6
LONDON : 1977

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1. INFRAGENERIC CLASSIFICATION

BY

NORMAN KEITH BONNER ROBSON

Pp. 291–355 ; 9 *Text-figures*

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STUDIES IN THE GENUS *HYPERICUM* L. (GUTTIFERAE)

1. INFRAGENERIC CLASSIFICATION

By NORMAN K. B. ROBSON

ABSTRACT

A historical review of systematic work on *Hypericum* L. is followed by a discussion of evolutionary and nomenclatural problems that have been posed by it and a consideration of evolutionary trends in the genus. A provisional sectional classification with full synonymy is given, along with a provisional key to the sections.

INTRODUCTION

IN THIS paper, the first of a series of studies which, it is hoped, will culminate in a monograph of *Hypericum* L., the delimitation of the genus is outlined and a provisional sectional classification and key is given.

HISTORICAL

The name *hypericum* (ὑπέρεικον) was given by the Greeks to a plant or plants that they hung above their religious figures to ward off evil spirits (ὑπέρ–above), (ἐικον–image). Exactly which species was so used is not known with certainty, although various authors have suggested that it was *Hypericum empetrifolium* Willd. or *H. triquetrifolium* Turra (*H. crispum* L.). The earliest use of the name that has been traced so far is in the 2nd century B.C. by Nikander (Alexipharmaca, V, line 603) :

> *τῷ δ'ὁτὲ μὲν σμύρνης ὀδελοῦ πόρε διπλόον ἄχθος,*
> *ἄλλοτε δ'ὁρμίνοιο νέην χύσιν, ἄλλοτε κόψαις*
> *οὐρείην ὑπερέικον, ὅθ' ὑσσώπου ὀροδάμνους.*

> 'And take a double 12-grain dose of myrrh, or a fresh draught of horminium, or pounded mountain hypericum or branches of hyssop.'

The qualification 'mountain' here suggests that more than one species of *Hypericum* may have been recognized at that time.

The name was mentioned by Dioscorides (Mat. Med., l. 3 cap. 171), Galen (12, 148) and Pliny (26. s. 53) ; and the illustration of *Uperikon* in the Codex Aniciae Iulianae nunc Vindobonensis : 357r, representing the traditional use of the name, clearly portrays *H. empetrifolium.* Dioscorides also described *Askuron* (M.M. 3, 172) – possibly *H. triquetrifolium* Turra or *H. perforatum* L. – and *Androsaimon* (M.M. 3, 173) – probably *H. perfoliatum* L. The last name appears to have been given to any species that had red sap or glandular secretion that stained the fingers like blood. The description of *Koris* (M.M. 3, 174) also suggests *H. empetrifolium.*

The name *Hypericum* was also used by various 16th and 17th century authors; but Tournefort (1700 : 254, t. 131) was the first one to give a generic description of *Hypericum*, which he characterized by a trimerous gynoecium in contrast to the pentamerous gynoecium of his *Ascyrum* (Tournefort, 1700 : 256, t. 131). His illustration of *Ascyrum* could be of *H. ascyron* L., from E. Asia and eastern N. America, as it shows the partly united styles of that species, although the apparently deciduous petals and stamens that are also portrayed do not fit it. On the other hand, he includes references among his list of species of *Ascyrum* to two that have a trimerous or rarely tetramerous gynoecium, viz. *H. richeri* Vill. subsp. *burseri* (DC.) Nyman (*Ascyrum magno flore* C. B. Pin. 280, Prodr. 130) and *H. olympicum* L. (*Ascyrum exiguo folio, flore magno*. Hypericon Olympi Montis Whel. Itin.). Tournefort also excluded some other species now normally included in *Hypericum*, making separate genera for those with baccate fruits (*Androsaemum*) and whorled leaves (*Coris*).

Linnaeus in his *Genera Plantarum* (1737) recognized the two genera *Hypericum* (5 petals, numerous stamens) and *Ascyrum* (4 petals, numerous stamens). In the *Species Plantarum* (1753) and the fifth edition of the *Genera Plantarum* (1754), he added *Sarothra* (5 petals, 5 stamens).

Miller (1754) also recognized *Ascyrum*, but in the sense of Tournefort (i.e. species with a 5-merous gynoecium), not of Linnaeus (i.e. species with a 4-merous perianth), syntypes being *H. calycinum* L. and *H. balearicum* L. Whilst he gave a description of the former species, he used for it the name *Ascyrum magno flore* C. B[auhin]. P[inax], which, however, refers to *Hypericum richeri* subsp. *burseri*. Linnaeus (1753 : 784) wrongly included Bauhin's name under *H. olympicum* L. This disagreement between Linnaeus and Miller eventually resulted in a certain amount of confusion. Miller also distinguished *Androsaemum* (species with baccate fruits), but this generic name was not validly published until the following year (Duhamel du Monceau, 1755 : 53).

Other genera in the *Hypericum* affinity were introduced by Colden (in Garden, 1756 – *Gardenia*, non *Gardenia* Ellis, nom. cons.), Adanson (1763 – *Komana, Knifa, Hypericoides, Elodes*) and Linnaeus fil. (1781 – *Brathys*). Unfortunately, A. L. de Jussieu (1789 : 255), in observing that *Hypericum* might be divisible into five separate genera, listed one of them as '*Elodea* Adans.', and this name, as a generic name or sectional epithet, came to be treated as distinct from *Elodes* and as referring to a different taxon (for fuller discussion see below, pp. 305–306).

The first treatment of the whole genus, however, was by Choisy (1821), whose synoptic monograph of the Hypericineae contained seven genera, of which three (*Androsaemum, Hypericum* and *Ascyrum*) comprised his Tribus II^{a} Hypericeae and together represent *Hypericum* in its current sense, except that he included the species now placed in *Triadenum* Raf. (i.e. *Gardenia* Colden non Ellis). The other two genera in Choisy's Hypericineae vera (*Vismia* Vand., *Haronga* Thouars) comprised Tribus I^{a} Vismieae, whilst the remaining two (*Carpodontos* Labill., *Eucryphia* Cav.) were classified as Hypericineae anomala. *Androsaemum* was monotypic (*H. androsaemum* L.) and *Ascyrum* was used in the Linnaean sense. The *Ascyrum* of Tournefort, Miller and others was treated, under the epithet

Ascyreia Choisy, as the first of his four sections of *Hypericum* and contained species with usually terminal flowers, unequal entire sepals, numerous stamens and 3–5 styles. The other sections were: *Brathys* (L.f.) Choisy (axillary flowers, equal entire sepals, numerous stamens, 3–5 styles), *Perforaria* Choisy (axillary flowers or panicles, equal and entire or dentate sepals, numerous stamens, usually 3 styles), and *Elodea* Choisy (axillary or terminal flowers, equal entire sepals, 9–15 stamens, 3 styles). The last section, based by Choisy on '*Elodea* Juss.', is now usually treated as the genus *Triadenum* Raf. Choisy's contribution to De Candolle's *Prodromus* (Choisy, 1824) is a somewhat extended version of his 1821 treatment.

In Spach's account of the Hypericaceae (Spach, 1836b, c), the family was divided into two tribes: Desmostemoneae (with 'glands' between the stamen fascicles) and Hypericeae (without such 'glands'). The Hypericeae, divided into 17 genera (13 of them new), corresponded to Choisy's Hypericeae excluding the species with interstaminal 'glands' (*Hypericum aegypticum* L., *H. elodes* L. and those placed by Choisy in *Hypericum* sect. *Elodea*). Each of these three excluded taxa was treated by Spach as a separate genus and the three genera (*Triadenia*, *Elodes* and *Elodea*) constituted his Elodeineae, one of the 'sections' (a misplaced term) into which he divided his tribe Desmostemoneae. His other two 'sections' of this tribe were the Vismineae and the Tridesmineae, both consisting of genera that have always been regarded as distinct from *Hypericum*. The fragmentation of this genus was continued by Jaubert & Spach (1842), who described two more genera in the group.

Meanwhile, in 1837, Rafinesque-Schmaltz, who had in 1808 published as a *nomen nudum* the generic name *Triadenum*, not to be confused with *Triadenia* Spach, gave it valid publication as a name for the genus that Spach had called *Elodea*.

Endlicher (1840) reduced most of Spach's genera to infrageneric taxa in *Hypericum*, thus laying the foundation for Keller's (1893, 1925) later accounts of the genus. Unfortunately, as Brizicky (1969) has pointed out, he did not specify their rank, and this makes for problems in citation. Endlicher distinguished *Ascyrum* L. (4-merous perianth) and '*Elodea* Adans.' [sic!] (with interstaminal 'glands', i.e. *Triadenia*, *Elodes* and *Elodea* of Spach), but placed all the remaining genera of Spach's Hypericeae in *Hypericum*.

Blume (1856) adopted Spach's generic concept except for *Eremanthe*, which he treated as one of two sections of *Norysca* Spach.

Bentham (1862) followed Endlicher's broad concept of *Hypericum*, but went further by including in it those species that Endlicher had referred to *Elodea*. Keller's (1893, 1925) treatments are essentially elaborations of Endlicher's work, except that he, like Bentham, did not recognize *Elodea* in Endlicher's sense as a separate genus but included it in *Hypericum*, thus reducing the Hypericeae to two Linnaean genera, *Hypericum* and *Ascyrum*.

Stefanoff (1932–34, 1933) made a detailed revision of the species of Europe, W. Asia, N. Africa and Macaronesia, describing 40 sections of which 22 were new. His view of *Hypericum* was broad, in that he followed Keller in including all three species with interstaminal glands then known from the area, each in its own section. His new sections, however, were described only, not typified, and only the species of the area under consideration were cited. Subsequent authors dealing with other

Table I

Comparison of classifications of *Hypericum* and allied genera

Spach (1836a, b), Jaubert & Spach (1842)	Engler (1925), Keller (1925)	Kimura (1951)
Hypericaceae Juss.	Guttiferae subfam. Hypericoideae Engl.	Hypericaceae Juss.
Trib. Desmostemoneae Spach		Subfam. Vismioideae Y. Kimura
'Sect'. Vismineae Spach	Trib. Vismieae Choisy	Trib. Vismieae Choisy
'Sect.' Tridesmineae Spach	Trib. Cratoxyleae Benth.	Trib. Cratoxyleae Benth.
	Trib. Hypericeae Choisy	
'Sect.' Elodeineae Spach		Trib. Elodeae Endl.
	Hypericum L.	
Elodea Juss. (non Michx.)	Sect. *Elodea* (Juss.) Choisy	*Triadenum* Raf.
Elodes Adans.	Sect. *Elodes* (Adans.) Syme	*Spachelodes* Y. Kimura
Triadenia Spach	Sect. *Triadenia* (Spach) R. Keller	*Elodes* Adans p.p.
Adenotrias Jaub. & Spach	Sect. *Adenotrias* (Jaub. & Spach) R. Keller	*Elodes* Adans p.p.
Trib. Hypericeae Choisy		Subfam. Hypericoideae Engl.
'Sect.' Androsaemineae Spach		Trib. Androsaemeae Y. Kimura
Androsaemum (Duham.) Spach	Sect. *Androsaemum* (Duham.) Godr.	*Androsaemum* (Duham.) Spach
		Trib. Hypericeae Choisy
Psorophytum Spach	Sect. *Psorophytum* (Spach) R. Keller	*Psorophytum* Spach
Norysca Spach	Sect. *Norysca* (Spach) R. Keller p.p.	*Norysca* Spach p.p.
Eremanthe Spach	Sect. *Eremanthe* (Spach) Boiss.	*Norysca* Spach p.p.
	Sect. *Norysca* (Spach) R. Keller p.p.	*Takasagoya* Y. Kimura
		Hypericum L.
Campylosporus Spach	Sect. *Campylosporus* (Spach) R. Keller	Sect. *Campylosporus* (Spach) R. Keller
Roscyna Spach	Sect. *Roscyna* (Spach) R. Keller	Sect *Roscyna* (Spach) R. Keller
Campylopus Spach	Sect. *Campylopus* (Spach) Boiss.	Sect. *Campylopus* (Spach) Boiss.
'Sect.' Hyperineae Spach		
Webbia Spach	Sect. *Webbia* (Spach) R. Keller	Sect. *Webbia* (Spach) R. Keller
	Sect. *Euhypericum* Boiss.	
Olympia Spach	Subsect. *Olympia* (Spach) Boiss.	Sect. *Olympia* (Spach) Stef.

Hypericum L.		
Sect. *Holosepalum* Spach p.p.	Subsect. *Homotaenium* R. Keller p.p.	Sect. *Homotaenium* (R. Keller) Y. Kimura p.p.
Sect. *Holosepalum* Spach p.p.	Subsect. *Oligostema* Boiss.	Sect. *Homotaenium* (R. Keller) Y. Kimura p.p.
Sect. *Adenosepalum* Spach	Subsect. *Homotaenium* R. Keller p.p.	Sect. *Homotaenium* (R. Keller) Y. Kimura p.p.
Sect. *Taeniocarpium* Jaub. & Spach	Subsect. *Homotaenium* R. Keller p.p.	Sect. *Homotaenium* (R. Keller) Y. Kimura p.p.
Sect. *Helianthemoides* Spach	Subsect. *Homotaenium* R. Keller p.p.	Sect. *Homotaenium* (R. Keller) Y. Kimura p.p
Sect. *Milleporum* Spach	Subsect. *Heterotaenium* R. Keller	Sect. *Milleporum* Spach
Sect. *Drosocarpium* Spach	Subsect. *Drosocarpium* (Spach) Boiss.	Sect. *Drosocarpium* Spach
Sect. *Coridium* Spach	Subsect. *Coridium* (Spach) Boiss.	Sect. *Coridium* Spach
Sect. *Crossophyllum* Spach	Subsect. *Crossophyllum* (Spach) Boiss.	Sect. *Crossophyllum* Spach
Sect. *Arthrophyllum* Jaub. & Spach	Subsect. *Arthrophyllum* (Jaub. & Spach) Boiss.	Sect. *Arthrophyllum* Jaub. & Spach
Sect. *Triadenioides* Jaub. & Spach	Subsect. *Triadenioides* (Jaub. & Spach) Boiss.	?
'Sect.' Drosanthineae Spach		
Eremosporus Spach	Subsect. *Homotaenium* R. Keller p.p.	Sect. *Homotaenium* (R. Keller) Y. Kimura
Drosanthe Spach	Subsect. *Homotaenium* R. Keller p.p.	Sect. *Homotaenium* (R. Keller) Y. Kimura
Thymopsis Jaub. & Spach	Subsect. *Homotaenium* R. Keller p.p.	Sect. *Homotaenium* (R. Keller) Y. Kimura
	Sect. *Thasium* Boiss.	[in sect. *Roscyna*]
	Sect. *Humifusoideum* R. Keller	?
'Sect.' Brathydineae Spach		Trib. Sarothreae Y. Kimura
Myriandra Spach	Sect. *Myriandra* (Spach) R. Keller	*Myriandra* Spach
Brathydium Spach	Sect. *Brathydium* (Spach) R. Keller	*Brathydium* Spach
Brathys Mutis ex L. f.	Sect. *Brathys* (Mutis ex L. f.) Choisy	*Sarothra* L.
		Trib. *Ascyreae* Y. Kimura
Isophyllum Spach	*Ascyrum* L. p.p.	*Ascyrum* L. p.p.
'Sect.' Ascyrineae Spach		
Ascyrum L.	*Ascyrum* L. p.p.	*Ascyrum* L. p.p.

NOTE: The taxa placed on the same line are not necessarily coextensive, but they are cotypal.

regions have therefore tended to ignore Stefanoff's sections. In particular, Gorschkova (1949) accepted Keller's subdivision of sect. *Euhypericum* Boiss. into seven subsections, but placed the Russian species of these subsections under 23 new series names, all of which have only Russian descriptions and hence are not validly published.

Kimura (1951) made a partial return to Spach's view of the Hypericaceae, but with a modified nomenclature. His subfamilies Vismioideae and Hypericoideae are coextensive with Spach's tribes Desmostemoneae and Hypericeae respectively, as is shown in Table 1. In addition, within the Hypericoideae, Kimura raised to generic rank a number of Keller's sections of *Hypericum* (*Androsaemum*, *Psorophytum*, *Norysca*, *Myriandra*, *Brathydium* and *Sarothra* (sect. *Brathys*)), as well as including *Ascyrum* and one genus described by himself, *Takasagoya*.

PROBLEMS POSED BY PREVIOUS CLASSIFICATIONS

A study of Table 1 will reveal several major differences of opinion about rank, relationships and nomenclature, all of which must be reconciled before any new classification can be proposed. It will also suggest some more general questions. Apart from differences in ranking, these problems are essentially five in number:

(1) Should the group as a whole be accorded family status or included in the Guttiferae?

(2) Should the 'Elodes' group (with interstaminal 'glands') be included in *Hypericum* or are its affinities with the Vismieae and Cratoxyleae?

(3) Kimura's tribes Sarothreae and Ascyreae (and the equivalent groups of Spach and Keller) contain species in which the androecium is said to be afasciculate, whilst the rest of the groups mentioned in the table have a fasciculate androecium. Which is the primitive condition in the genus?

(4) All three classifications agree in separating *Ascyrum* L. from *Hypericum*. Is tetramery in the perianth a monophyletic development and, if so, is the group with such a perianth worthy of generic rank?

(5) What is the type of *Elodes* Adanson and is *Elodea* Juss. a distinct name?

Family or subfamily?

Authors have agreed that the taxa included in Table 1 form a natural group; but, whereas Spach (1836a, b), Bentham (1862) and Kimura (1951) treated this group as a separate family, Engler (1893, 1925) included it in the Guttiferae as a subfamily coordinate in rank with the Kielmeyeroideae, Calophylloideae, Moronoboideae and Clusioideae. Bentham placed the African monotype *Endodesmia calophylloides* Benth. in the Hypericaceae; but Engler (1888) transferred it to the Calophylloideae as a separate tribe, Endodesmieae. Along with a closely allied monotype from Zaire, *Lebrunia bushiae* Staner, it is quite out of place in the Hypericaceae, as both genera have multinerved leaves, a 1-seeded drupaceous fruit and (at least *Endodesmia*) a large seed with thick fleshy cotyledons. On the other hand, all these characters (as well as the complete absence of staminodes) fit well in the Calophylloideae, where I believe that *Endodesmia* and *Lebrunia* belong.

The remaining group, without these two genera, is a natural one falling into three subgroups which can be defined, leaving the 'Elodes' group out of account for the present, as follows (Table 2) :

TABLE 2

Characters of tribes of the Hypericoideae (excluding the 'Elodes' group)

	VISMIEAE	CRATOXYLEAE	HYPERICEAE
FRUIT	Berry or drupe	Capsule	Capsule (rarely subbaccate or tricoccoid)
SEED	Not winged	Winged	Rarely winged, sometimes keeled
INTERSTAMINAL GLANDS	Present	Present	Absent
PETAL COLOUR	White, yellow or orange	White or pink	Yellow to orange (rarely red, crimson or white)

The main characters by which these three tribes differ from all the rest of the Guttiferae sensu Engler are :

(i) The possession of free styles (except in some species of *Hypericum*) ;

(ii) the occurrence of black glands containing hypericin (except in some species of *Hypericum*) ;

(iii) the occurrence of the herbaceous habit (in some species of Cratoxyleae and Hypericeae) ;

(iv) the predominance of translucent glands rather than canals.

All these distinctions, however, are only partial. Indeed, the transitions from united to free styles, absence to presence of black glands, trees to herbs and glandular canals to dots can all be observed in *Hypericum* itself. It seems clear, therefore, that the appropriate rank for the taxon that includes the tribes Vismieae, Cratoxyleae and Hypericeae is that of a subfamily of the Guttiferae – the Hypericoideae – coordinate with the Calophylloideae, Moronoboideae and Clusioideae. The subfamily Kielmeyeroideae is probably better removed from the Guttiferae to the Bonnetiaceae (Maguire, 1972 ; Hutchinson, 1973). However, my recent research has indicated that the tribes of the Hypericoideae are less closely interrelated than I had thought and that they may have originated independently from pre-Bonnetiaceous ancestors. If this is so, then the Guttiferae should probably be enlarged to include the Bonnetiaceae.

The 'Elodes' group – primitive or specialized?

As the historical review showed, there has been much disagreement over the systematic position of Keller's first four sections of *Hypericum* (sects *Elodea, Elodes,* *Triadenia* and *Adenotrias*), the view adopted depending on whether the authors regarded their anomalous floral structure as more or less important than their undoubted vegetative resemblances to *Hypericum*.

Keller's four sections can be reduced to three, as sections *Triadenia* and *Adenotrias* are very closely allied, differing only in having (i) persistent petals, usually 1-flowered inflorescences and ovary loculi with seeds in three rows (*Triadenia*) or (ii) deciduous petals, 3 – 8-flowered inflorescences and ovary loculi 2-seeded (*Adenotrias*). The resemblances between these two groups – they both comprise glabrous ± microphyllous Mediterranean shrubs with nectariferous petal appendages, fleshy hypogynous 'glands', dimorphically heterostyled flowers and carunculate seeds – are so much greater than their differences that it seems appropriate to unite them. *Triadenia* is the correct (earlier) name if the united taxon is treated as a genus, but *Adenotrias* must be used at the sectional level, and the rank adopted depends on the view taken of its affinities.

This united taxon, which for convenience will be referred to as a section of *Hypericum*, and the other two sections of the 'Elodes' group are all well distinguished from one another, and it is clear that their relationships are by no means close (Table 3). Sect. *Elodea* differs from all other *Hypericum* species in having petals imbricate but not contorted in bud and a chromosome number of n = 19, and from nearly all in its pink or white petals and axillary flowers. In *Hypericum*, the petals are always contorted in bud and nearly always yellow, often more or less red-tinged. Only very rarely is the yellow flavone absent, giving white or pinkish-tinged petals (*H. aviculariifolium* Jaub. & Spach var. *albiflorum* Hub.-Mor.), or the red pigment so intense as to give orange-red to crimson petals (*H. capitatum* Choisy var. *capitatum*). The inflorescence in *Hypericum* is never truly axillary, and the basic chromosome number varies from 7 to 12, never to 19 (Robson & Adams, 1968).

For these and other reasons (cf. Robson, 1956), it seems appropriate to remove sect. *Elodea* from *Hypericum* altogether. If this is done, it fits into the system very well as a herbaceous derivative of *Cratoxylum* Blume, an Indo-Malayan genus of the Cratoxyleae. All the features of *Triadenum* Raf. (i.e. *Hypericum* sect. *Elodea*) that are anomalous in *Hypericum* are typical of *Cratoxylum* except the chromosome number ; but this difference may not be significant as only one chromosome count of one species of *Cratoxylum* has been published, n = 7 (see Robson & Adams, 1968). The relative distributions of the two genera agree with the hypothesis that one is derived from the other. Apart from the very closely allied genus *Eliea* Cambess., endemic to Madagascar (Baas, 1970), the Cratoxyleae have hitherto consisted only of *Cratoxylum*, which occurs from Celebes and the Lesser Sunda Islands to S. China and Assam (Gogelein, 1967). The distribution of *Triadenum* (Khasia, N.E. Asia, eastern N. America) is quite in keeping with the idea that it has spread into temperate regions while evolving a herbaceous habit. The species of *Triadenum* all have pink or reddish petals except for the one that occurs in Khasia (Assam) and is geographically closest to *Cratoxylum* (*T. breviflorum* (Wall. ex Dyer) Y. Kimura), in which they are white. This species has recently been recorded from Taiwan (Robson, 1976), a discovery that helps to bridge the gap in distribution between Assam, on the one hand, and Japan, Korea and adjacent

TABLE 3

Comparison of members of the 'Elodes' group of *Hypericum*

	SECT. *Adenotrias*	SECT. *Elodes*	SECT. *Elodea*
HABIT	low shrubs	rhizomatous herb	rhizomatous herbs
RED GLANDS	absent	present	absent
INDUMENTUM	absent	present	absent
LEAVES	sclerophyllous	herbaceous	herbaceous
INFLORESCENCE	terminal	terminal	axillary
SEPAL MARGIN	entire	gland-fringed	entire
PETAL AESTIVATION	contorted	contorted	imbricate only
PETAL COLOUR	yellow	yellow	pink or white
PETAL DURATION	variable	persistent	deciduous
PETAL APPENDAGE	entire	trifid	absent
HYPOGYNOUS 'GLANDS'	fleshy	scale-like	scale-like
HETEROSTYLY	present	absent	absent
PLACENTATION	axile	parietal	axile
SEEDS PER PLACENTA	numerous or 2	numerous	numerous
TESTA	pitted	scalariformly striate	pitted
CARUNCLE	present	absent	absent
CHROMOSOMES (2n)	20	32	38
HABITAT	dry rocks	aquatic or subaquatic	marshes
DISTRIBUTION	Mediterranean	W. Europe, Azores	E. Asia, eastern N. America

Siberia on the other. (For a map of the distribution of the Cratoxyleae, excluding Taiwan, see Robson, 1972.)

A further link between S.E. Asia and America in the tribe Cratoxyleae is provided by two species from southern Mexico that have wrongly been included in *Hypericum* (*H. matudai* Lundell and *H. calcicola* Standley & Steyerm.). These species have flowers with some characters of *Triadenum* (pink petals and an androecium of three fascicles, each of three stamens, alternating with three hypogynous 'glands'), but they differ in being much-branched shrubs with smaller leaves and flowers, filaments free to near the base, and seeds with a small caruncle (at least in *H. calcicola*). These two species constitute a separate genus, *Thornea*, very recently described as new by Dr D. Breedlove and Dr E. McClintock (1976), which would seem to have been derived directly from *Cratoxylum*.

When *Triadenum* and the new genus, *Thornea*, are excluded, the species of the 'Elodes' group look superficially like true Hypericums although, as Table 3 indicates, the members of the two remaining sections differ markedly in many respects other than the possession of petal appendages, hypogynous 'glands' and (not mentioned in Table 3) stamen filaments united to above the middle. If these specialized characters and the heterostyly and carunculate seeds are ignored, then sect. *Adenotrias* agrees well with sects *Triadenioides* and *Heterophylla*, which also contain dwarf microphyllous shrubs of the eastern Mediterranean. In the same way, *H. elodes*, the one species of sect. *Elodes*, agrees well with sect. *Adenosepalum*, which includes two species of damp habitats from areas adjacent to that of *H. elodes* (*H. caprifolium* Boiss. from S.E. Spain and *H. coadunatum* Chr. Sm. from the Canary Islands and N. Africa). Both these species have pubescent stems and leaves and bear a strong resemblance to *H. elodes*, although in both the leaves are perfoliate, not free as in *H. elodes*. (For distribution maps of all the above taxa, see Robson, 1972).

It seems clear, then, that sects *Adenotrias* and *Elodes* are derivatives of *Hypericum* itself, not of the shrubby genera in the Vismieae and Cratoxyleae, and that their various morphological anomalies are developments from within *Hypericum*. A study of the floral anatomy of these groups supports this view. Whereas the sterile stamen fascicles in the Vismieae and Cratoxyleae (including *Triadenum*) have vascular connections with the stele, those of the hypogynous 'glands' in *Hypericum aegypticum* L. (the type species of *Triadenia*) and *H. elodes* have none (Robson, 1956, 1972).

If the various adaptations in the flowers of sects. *Adenotrias* and *Elodes* are regarded from a functional viewpoint, they can all be shown to be modifications towards specialized insect pollination. Thus the sepals in both sections are erect, so that the bases of the petals form a tube and the upper parts spread out, giving the effect of a rotate tubular corolla. In this connection, it is noteworthy that these species with a pseudo-tubular corolla are the only ones in the genus to have the stamen filaments united for more than a short way above the base. The petal appendages, which appear to be nectariferous, are unknown elsewhere in the Guttiferae except in *Cratoxylum* sects *Triadesmos* and *Isopterygium*, where they also seem to have arisen 'de novo' along with dimorphic heterostyly.

Hochreutiner (1918) showed that the hypogynous bodies in the Guttiferae are not glandular and do not secrete nectar. In *Hypericum elodes*, *Psorospermum* (Vismieae) and *Eliea* (Cratoxyleae) at least, and probably also in *Cratoxylum*, they act like lodicules of grasses and help to expand the petals and sepals from the bud. When, furthermore, the dimorphic heterostyly in *Hypericum* sect. *Adenotrias* and the above-mentioned sections of *Cratoxylum* are taken into consideration, the conclusion is inescapable that there have been at least three independent evolutionary trends in the Hypericoideae towards specialized insect pollination, viz. in *Hypericum* sect. *Adenotrias*, *Hypericum* sect. *Elodes* and *Cratoxylum*.*

The question remains whether the 'lodicules' in *Hypericum* have no evolutionary forerunners at all (i.e. have truly arisen 'de novo') or are homologous with the hypogynous bodies in the rest of the Guttiferae (where they are staminodal in origin). When the functional aspects discussed above are taken into consideration, the latter would appear to be the more likely hypothesis, i.e. that the lodicules in *Hypericum* are staminodal. If this is so, then we have a case of evolutionary recall, in which organs which have atrophied during the course of evolution have been subsequently regained but perform a function different from their original one. (For a more detailed discussion of these ideas see Robson, 1972).

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* Dimorphic heterostyly also occurs in several species of *Vismia* (Robson, ined.).

The fasciculate androecium – primitive or specialized?

In *Hypericum* sensu Keller there are four sections in which the stamens are described as either all free or all united at the base to form a short tube, not in fascicles. These are sects *Campylopus*, *Myriandra*, *Brathydium* and *Brathys* (Table 1). The monadelphy in sect. *Campylopus*, a section which comprises only *H. cerastoides* (Spach) N. Robson (*H. rhodoppaeum* Friv.), is clearly secondary. Apart from the fact that the monadelphy is not constant, so that flowers with five, four or three stamen fascicles occur not infrequently, *H. cerastoides* forms a morphological link between two sections (*Olympia* and *Origanifolia*) in which all the species have fasciculate androecia. That the stamens of *H. cerastoides* are also basically fasciculate is borne out by a study of the floral vasculature (Robson, 1956).

The remaining sections fall into two groups. Sects. *Myriandra* and *Brathydium* contain species with appressed styles, small stigmas and a mass of apparently free stamens, whilst in sect. *Brathys* the styles are divergent with often capitate stigmas and stamens arising from a narrower zone of the receptacle. An investigation of the floral vasculature of these sections (Robson, 1956) showed that the numerous stamens in the large-flowered species are always innervated from five antepetalous branching vascular trunks, just like those serving the androecia of the 5-fascicled species in other sections. The vascular pattern becomes somewhat irregular in the small-flowered herbaceous species of sect. *Brathys* subsect. *Spachium*, as it does in small-flowered herbs elsewhere in the genus; but all the variation can be explained in terms of a basically isomerous, pentamerous flower with numerous stamens in each of the five fascicles. The morphological trends in *Hypericum* also make sense only if such a flower is taken to be primitive.

An indication of the possible cause of the disappearance of fascicles in sects *Myriandra*, *Brathydium* and *Brathys* resulted from a study of their floral anatomy (Robson, 1956). In the first two sections the floral receptacle is relatively narrow, the androecial zone is relatively broad and the vascular traces are close together, suggesting that evolution has resulted in a crowding of the stamen fascicles. In contrast, the floral receptacle in the large-flowered species of sect. *Brathys* is relatively broad, the androecial zone is relatively narrow and the vascular traces are spaced out, suggesting that evolution has resulted in the 'squeezing out' of the stamen fascicles to form a continuous ring. This hypothesis is supported by the observation that, in more advanced species of sect. *Spachium* in which there are fewer stamens (hence making a complete ring less easily formed), the fascicles are sometimes visible. In the extreme case of *H. gentianoides* (L.) Britt., Sterns & Poggenb., an annual herb with scale-like leaves, each fascicle is often reduced to one stamen. It is not surprising, therefore, that Linnaeus placed this species in his Class Pentandria as the only species of the genus *Sarothra*.

The answer to the question posed in the heading to this section is clearly, then, that the fasciculate androecium in *Hypericum* is primitive, not specialized. The non-fasciculate and monadelphous states should be regarded as the result of the merging of fascicles equal in number to the petals and opposite them.

In many species of *Hypericum* with fasciculate androecia, however, the number of fascicles appears to be smaller than that of the petals. This phenomenon has been shown by various authors (Payer, 1857; Sachs, 1875; Hirmer, 1918; Breindl, 1934; Saunders, 1936, 1939; Robson, 1956) to be due to the merging of adjacent pairs of fascicles, with the result that the 4 fascicles are really $1+1+1+(2)$ and the 3 fascicles commonly found are $1+(2)+(2)$. These double fascicles are always opposite sepals (i.e. *between* petals), in fact opposite the last-formed sepals (sepal 5 in 4-fascicled flowers, sepals 4 and 5 in 3-fascicled ones). Although they are double structures, they have fewer than double the number of stamens found in the single fascicle (between sepals 1 and 3), and the one opposite sepal 5 is usually smaller than that opposite sepal 4 (cf. Saunders, 1936 : 316).

The genus Ascyrum *L. – distinct or not?*

Linnaeus distinguished *Hypericum*-like plants with four petals and four sepals as the genus *Ascyrum*, a view that was accepted by most subsequent workers up to and including Adams (1957). Spach (1836b) separated as the genus *Isophyllum* one species (*I. drummondii* Spach) which differed from the others in having four equal sepals instead of two small outer sepals and two large inner ones. In this generic separation he was followed by Small (1903), who, however, overlooked Spach's name and called the same species *Crookea microsepala* (Torrey & Gray) Small, based on *Ascyrum microsepalum* Torrey & Gray. Following observations that the American species of *Ascyrum* are closely related to *Hypericum* sects *Myriandra* and *Brathydium* (Robson, 1956), these species of *Ascyrum* and *Isophyllum* were transferred to *Hypericum* by Adams & Robson (1961). Subsequently, Adams (1962) enlarged *Hypericum* sect. *Myriandra* to include all American species previously placed in sect. *Brathydium* or in *Ascyrum* or *Isophyllum*.

The word 'American' is used above because Dyer (1874) described a species from Sikkim with a tetramerous perianth as *Ascyrum filicaule*. Apart from the number of sepals and petals, however, this plant bears little resemblance to the American *Ascyrum* species. Thus, it is a dwarf herb with persistent petals, 'three' stamen fascicles, divergent styles, black glands on the anthers and petiolate leaves, whereas the American species are shrubs or shrublets with deciduous petals, an 'afasciculate' androecium, styles appressed at least at the base, no black glands, and sessile or amplexicaul leaves. *A. filicaule* is therefore not at all closely related to the American plants, but represents an independent development of tetramery in the perianth whorls. Its nearest relative would appear to be the Himalayan *Hypericum monanthemum* Hook. f. & Thoms. ex Dyer (sect. *Adenosepalum*), from which it is probably derived. Indeed, a study of the range of variation in the two 'species' has shown that, whereas the type of *H. monanthemum* falls with the variation range of *H. napaulense* Choisy, most of the specimens that have been determined as *H. monanthemum* cannot be distinguished from *Ascyrum filicaule*, apart from the number of petals and sepals. A validation of the last-mentioned name in *Hypericum*, as follows, is therefore required:

Hypericum filicaule (Dyer) N. Robson, *comb. nov.*
H. filicaule Hook. f. & Thomson, ex Dyer *in* Hook. f., *Fl. Brit. India*, **1** : 252 (1874) *nom. synon.*
Ascyrum filicaule Dyer, *loc. cit.*

The names Elodes *Adanson and* Elodea *Juss.*

In establishing the genus *Elodes*, Adanson (1763 : 444) cited Clus. Hist., a reference to *Ascyrum supinum* (ελοδης) of Clusius, Rar. Pl. Hist. App. Alt. (1601). Clusius gives a good description of *Hypericum elodes* L., which can therefore be taken as one element of Adanson's protologue. As a synonym, however, Adanson also cited *Hypericum* 9. *Lin. Sp.* 784, which refers to the original description of *H. aegypticum* L. in *Species Plantarum* (1753). The name *H. elodes* L. did not appear until 1759, however, when Linnaeus's dissertation entitled *Flora Anglica* was republished (Amoen. Acad. **4** : 105) ; and so Adanson's omission of a reference to a Linnaean account of that species should not be over-emphasized. Indeed, in the Table at the end (Adanson, 1763 : 553) he cites '*Hypericum* Tour.' as a synonym of *Elodes*, and Tournefort (1700 : 255) mentions *H. elodes*, as *Hypericum palustre, supinum, tomentosum* (with references to Bauhin and Clusius), among his species of *Hypericum*. *H. aegypticum*, on the other hand, was unknown to Tournefort. There are, therefore, three elements in Adanson's protologue of *Elodes* of which one (the *Species Plantarum* citation) refers to *H. aegypticum* L. and the other two (the references to Clusius and Tournefort) indicate *H. elodes* L. These two species may thus be regarded as syntypes of *Elodes* Adanson, as Adanson's description applies to them both equally.

The first author to restrict *Elodes* to one of these species was Spach (1836a), who erected the genus *Triadenia* for *H. aegypticum* L. sensu lato, leaving only *H. elodes* L. in *Elodes* as *E. palustris* Spach. All subsequent authors have followed Spach's typification, whether they treated *Elodes* as a genus or a section, except Kimura (1951) and Greuter (1965), who decided in effect that the type must be *H. aegypticum*. Kimura's decision, which was apparently based on the argument that Adanson actually cited that species only, meant that Spach's *Elodes* required a new name. He therefore coined the name *Spachelodes*. If one takes the view that Adanson's *Elodes* has two syntypes of which one, *H. elodes* L., became the lectotype as a result of Spach's work, then Kimura's new genus is superfluous, a conclusion which appears to accord best with the facts explained above.

Interpretations of Adanson's genus have led to further confusion in that A. L. de Jussieu (1789 : 255), in observing that *Hypericum* was divisible into five separate genera, spelled the name of one of them '*Elodea* Adans.' Although this spelling is merely an orthographic change, it was adopted by Pursh (1814) and Choisy (1821, 1824), the latter reducing it to a section of *Hypericum*. In addition, however, Choisy followed Pursh in restricting his taxon to those American species with pink flowers that are now usually placed in *Triadenum* Raf. (1837). Spach (1836) restored Choisy's section to generic rank as '*Elodea* Adans. (non Michx.)', while, as mentioned above, placing *H. elodes* L. and *H. aegypticum* L. in *Elodes* Spach and *Triadenia* Spach respectively. He later added another new genus to this group, *Adenotrias* Jaub. & Spach (1842). Keller's (1893, 1925) treatment of these taxa as the first four sections of *Hypericum* essentially follows that of Choisy and Spach, as a list of his sectional names and cited authorities indicates: Sects. *Triadenia* (Spach) R. Keller [*H. aegypticum* L. sensu lato], *Adenotrias* (Jaub. & Spach) R. Keller [*H. russeggeri* Fenzl], *Elodes* (Adans.) R. Keller [*H. elodes* L.], *Elodea* (Juss.) Choisy [*Triadenum* Raf.].

Finally, it should be pointed out that, as *Elodea* Juss. (1789) is not a valid name, *Elodea* Michx. (1803 : 20), with its well-known species *E. canadensis* Michx., is not threatened by it.

RELATIONSHIPS AND EVOLUTIONARY TRENDS IN *HYPERICUM*

It is clear that, although Keller's classification contains some natural groups (e.g. sect. *Norysca*), others consist of several unrelated elements (e.g. sect. *Euhypericum*). An attempt has therefore been made to review the available evidence in order to detect evolutionary trends within *Hypericum*, in the hope that this would lead to a more natural system for the genus. This has involved original studies in morphology, distribution, floral vasculature and (to a limited extent) cytology, as well as a detailed examination of the relevant literature. In the process, provisional ideas about the direction of certain trends have had to be altered in the face of evidence from trends going in the opposite direction. For example, hypotheses that deciduous petals and stamens and divergent styles are primitive have proved untenable. In general, it has been possible to establish congruent trends throughout the genus. Certain characters, such as parietal placentation, deciduous petals and stamens, reduced basic chromosome numbers and modifications towards specialized entomophily, have apparently arisen independently more than once in the genus; but these parallelisms have rarely led to doubt about relationships. On the other hand, it has proved rather more difficult to sort out the several evolutionary lines in Keller's sect. *Euhypericum*, all of which have attained the floral structure of 'three' stamen fascicles, three divergent styles and axile placentation.

As a result of this review, the following trends can be postulated as consistent with the general picture of evolution in *Hypericum*:

Habit Trees→shrubs→perennial herbs→annual herbs.

Indumentum Absent→present (several independent occurrences).

Glands In general there are two types: (i) schizogenous cavities surrounded by secretory cells containing tannins, waxes or resins (Coutinho, 1950), which are described as pale or pellucid dots, lines or canals; (ii) masses of secretory cells without cavities, containing a waxy substance and often also *hypericin*, which are described as amber, red or black (or sometimes merely 'dark') dots or lines. The distribution of these two types is not completely independent; there seems to be a tendency for dark glands to occupy sites corresponding to those of pale glands in related species. No detailed comparative anatomical study of such a pair of related species appears to have been made. Pale canals appear to be generally more primitive than pale dots within the genus, whereas dark dots are apparently more primitive than dark streaks or lines. There is a tendency to increase the amount of dark secretory tissue in any one evolutionary line in which it has appeared; but this trend is occasionally reversed. Thus, some advanced members of sect. *Adenosepalum* (see p. 335) have fewer black glands than the primitive ones, whilst in sect. *Elodes* (apparently derived from sect. *Adenosepalum*) only red glands occur, indicating the presence of less dense concentrations of hypericin. (See Mathis (1963) for a detailed study of these secretions.)

Stem In general the trend runs as follows:

4-lined→2-lined→terete; but reversals are not uncommon.

Leaves

Sessile—┌→shortly petiolate
└→amplexicaul→perfoliate.
Deciduous (with basal articulation)→persistent (without basal articulation).
Opposite→whorled in 3s→whorled in 4s.
Venation parallel→reticulate.

Sepals

Unequal→equal (with occasional reversals).
Margin entire→dentate→ciliate→fimbriate.
Persistent→deciduous.
Free→united.

Petals

Persistent→deciduous (several independent occurrences).
Asymmetric→symmetric.

Perianth

5-merous→4-merous (two independent occurrences).

Stamen fascicles

5→4.
Free→variously united (2+1+1+1, 2+2+1, (5), (4)).
Persistent→deciduous (several independent occurrences).

Styles and placentae

5→2 (with rare reversals from 3 to 4 or 5).

Placentation

Loosely axile—┌→definitely axile.
└→parietal.

Ovules per placenta

∞→2 (? 1).

Seeds

Narrowly winged→carinate→cylindric.

Basic chromosome number

12→7 (? 6).

On the basis of the above and other less general trends, it has been possible to construct a revised scheme of classification for *Hypericum*. Fig. 1 is an attempt to show this in broad outline in relation to some of these trends, and the geographical relationships of the sections are indicated in Fig. 2. These geographical relationships fit a hypothesis that *Hypericum* evolved in Africa and spread to America, Asia and probably Australia before the disintegration of Gondwanaland. For discussions of the apparently anomalous distributions of some herbaceous species of sect. *Spachium*, see Robson (1972, 1973). In Figs 3–9, the distributions of the sections are shown, along with indications of morphological trends.

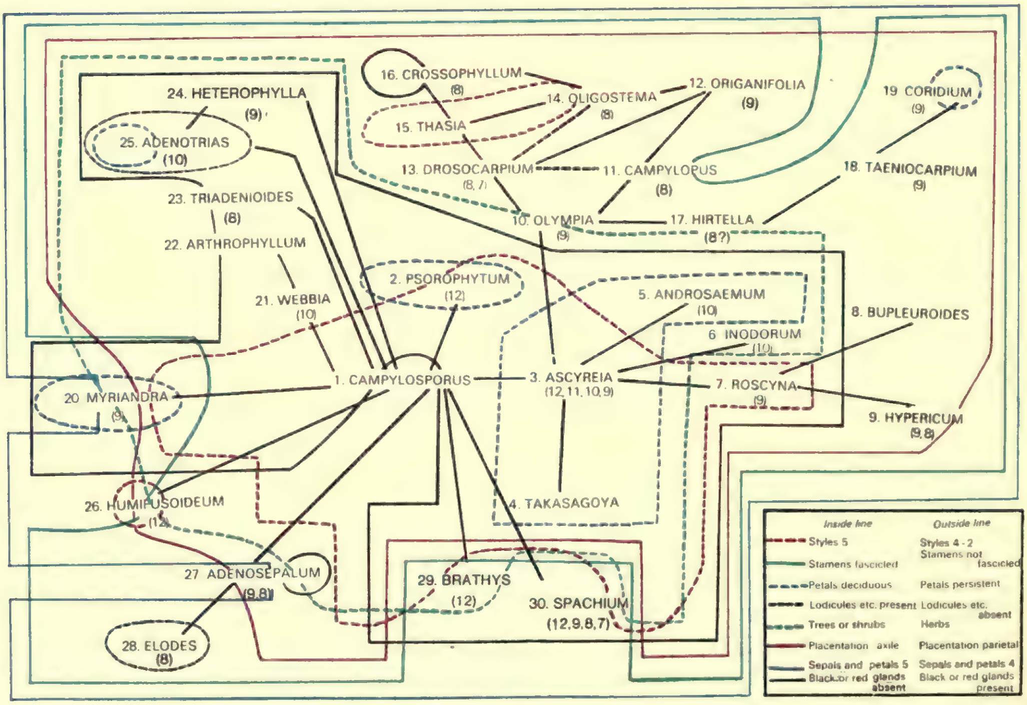

16. CROSSOPHYLLUM
(8)
12. ORIGANIFOLIA
(9)
14. OLIGOSTEMA
(8)
15. THASIA
19. CORIDIUM
(9)
24. HETEROPHYLLA
(9)
25. ADENOTRIAS
(10)
13. DROSOCARPIUM
(8,7)
11. CAMPYLOPUS
(8)
18. TAENIOCARPIUM
(9)
23. TRIADENIOIDES
(8)
10. OLYMPIA
(9)
17. HIRTELLA
(8?)
22. ARTHROPHYLLUM
2. PSOROPHYTUM
(12)
21. WEBBIA
(10)
5. ANDROSAEMUM
(10)
8. BUPLEUROIDES
6. INODORUM
(10)
20. MYRIANDRA
(9)
1. CAMPYLOSPORUS
3. ASCYREIA
(12,11,10,9)
7. ROSCYNA
(9)
9. HYPERICUM
(9,8)
26. HUMIFUSOIDEUM
(12)
4. TAKASAGOYA
27. ADENOSEPALUM
(9,8)
29. BRATHYS
(12)
30. SPACHIUM
(12,9,8,7)
28. ELODES
(8)
Inside line
Outside line
Styles 5
Styles 4 - 2
Stamens fascicled
Stamens not fascicled
Petals deciduous
Petals persistent
Lodicules etc. present
Lodicules etc. absent
Trees or shrubs
Herbs
Placentation axile
Placentation parietal
Sepals and petals 5
Sepals and petals 4
Black or red glands absent
Black or red glands present

FIG. 1. Proposed classification of *Hypericum*, showing suggested interrelationships and the distribution limits of certain characters. The numbers in parentheses are basic chromosome numbers.

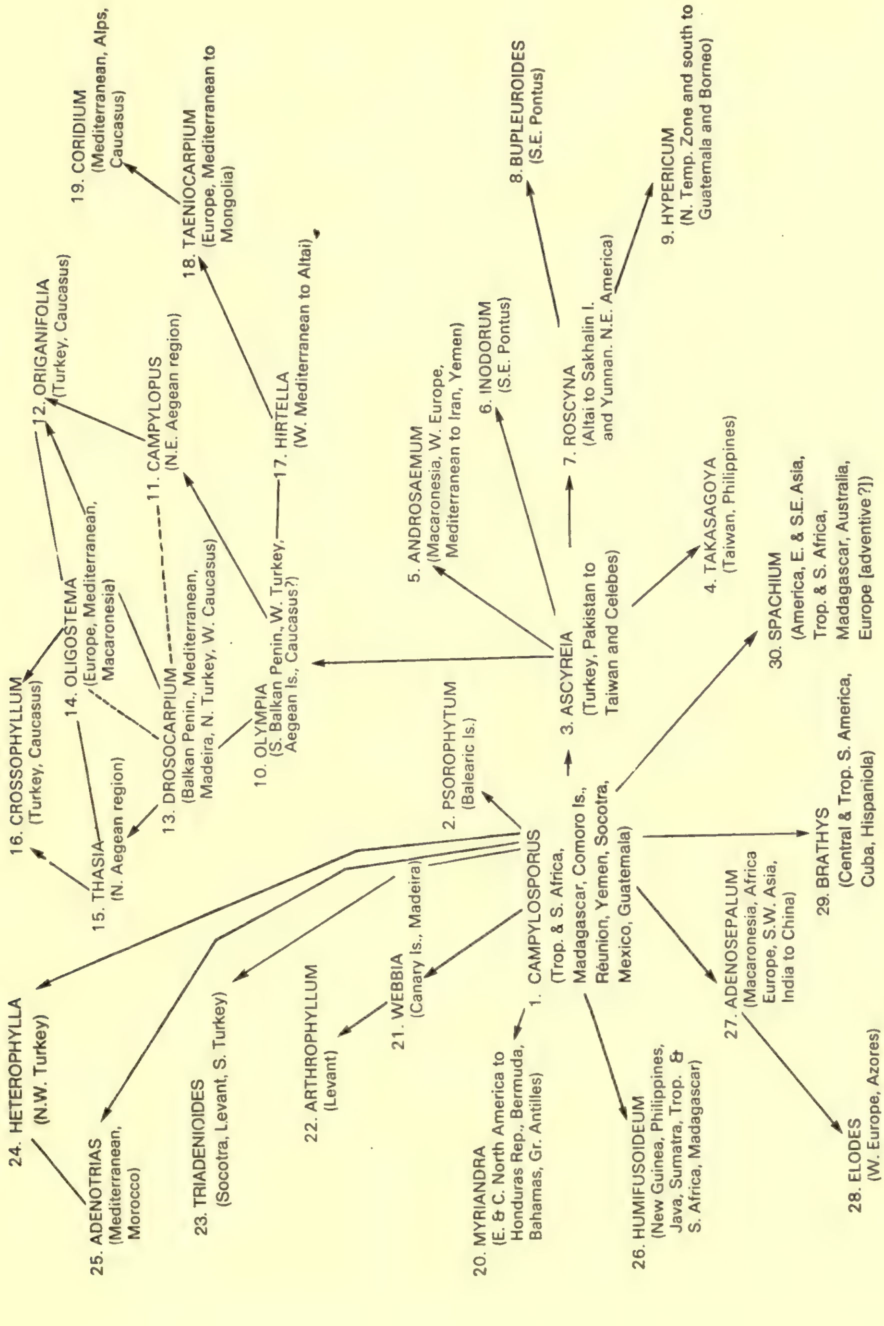

1. CAMPYLOSPORUS (Trop. & S. Africa, Madagascar, Comoro Is., Réunion, Yemen, Socotra, Mexico, Guatemala)
2. PSOROPHYTUM (Balearic Is.)
3. ASCYREIA (Turkey, Pakistan to Taiwan and Celebes)
4. TAKASAGOYA (Taiwan, Philippines)
5. ANDROSAEMUM (Macaronesia, W. Europe, Mediterranean to Iran, Yemen)
6. INODORUM (S.E. Pontus)
7. ROSCYNA (Altai to Sakhalin I. and Yunnan. N.E. America)
8. BUPLEUROIDES (S.E. Pontus)
9. HYPERICUM (N. Temp. Zone and south to Guatemala and Borneo)
10. OLYMPIA (S. Balkan Penin., W. Turkey, Aegean Is., Caucasus?)
11. CAMPYLOPUS (N.E. Aegean region)
12. ORIGANIFOLIA (Turkey, Caucasus)
13. DROSOCARPIUM (Balkan Penin., Mediterranean, Madeira, N. Turkey, W. Caucasus)
14. OLIGOSTEMA (Europe, Mediterranean, Macaronesia)
15. THASIA (N. Aegean region)
16. CROSSOPHYLLUM (Turkey, Caucasus)
17. HIRTELLA (W. Mediterranean to Altai)
18. TAENIOCARPIUM (Europe, Mediterranean to Mongolia)
19. CORIDIUM (Mediterranean, Alps, Caucasus)
20. MYRIANDRA (E. & C. North America to Honduras Rep., Bermuda, Bahamas, Gr. Antilles)
21. WEBBIA (Canary Is., Madeira)
22. ARTHROPHYLLUM (Levant)
23. TRIADENIOIDES (Socotra, Levant, S. Turkey)
24. HETEROPHYLLA (N.W. Turkey)
25. ADENOTRIAS (Mediterranean, Morocco)
26. HUMIFUSOIDEUM (New Guinea, Philippines, Java, Sumatra, Trop. & S. Africa, Madagascar)
27. ADENOSEPALUM (Macaronesia, Africa Europe, S.W. Asia, India to China)
28. ELODES (W. Europe, Azores)
29. BRATHYS (Central & Trop. S. America, Cuba, Hispaniola)
30. SPACHIUM (America, E. & S.E. Asia, Trop. & S. Africa, Madagascar, Australia, Europe [adventive?])

FIG. 2. Proposed classification of *Hypericum*, showing suggested interrelationships and the general distribution of each section. (Under sect. 5 *Androsaemum* for 'Yemen' read 'Asir'.)

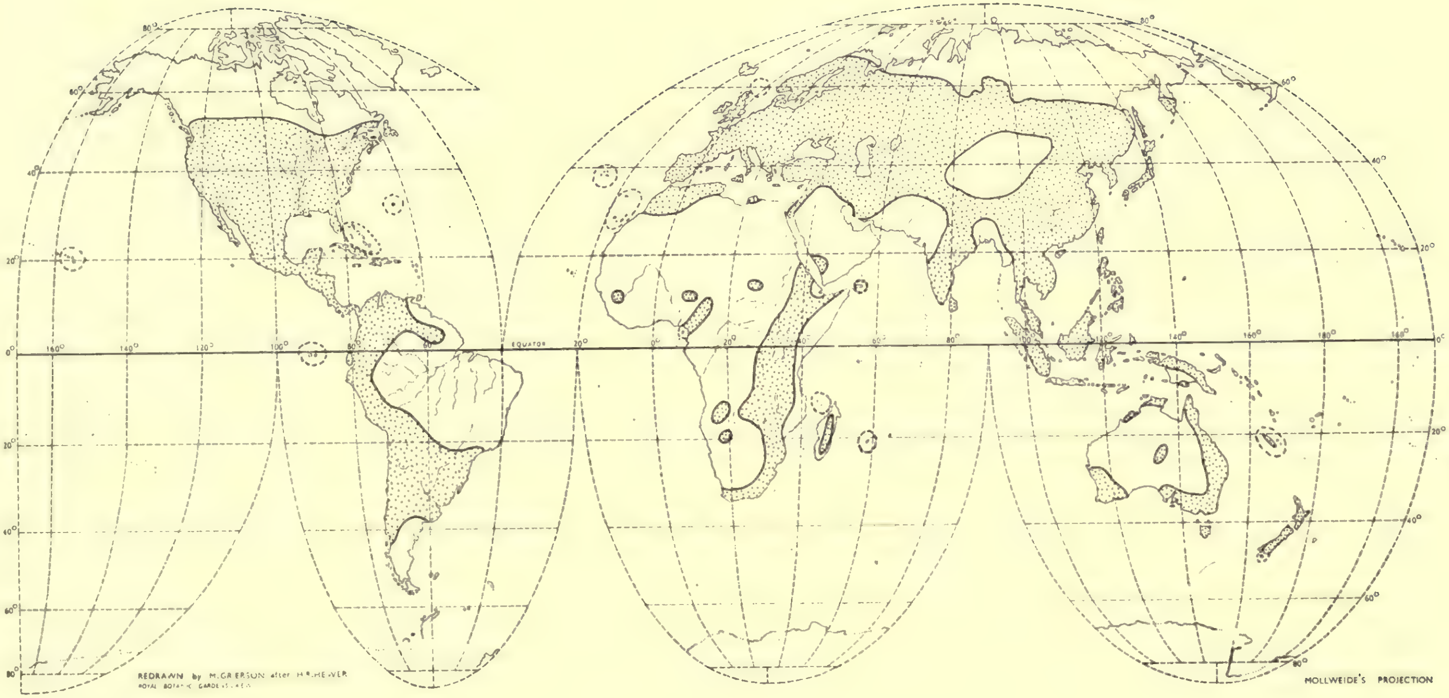
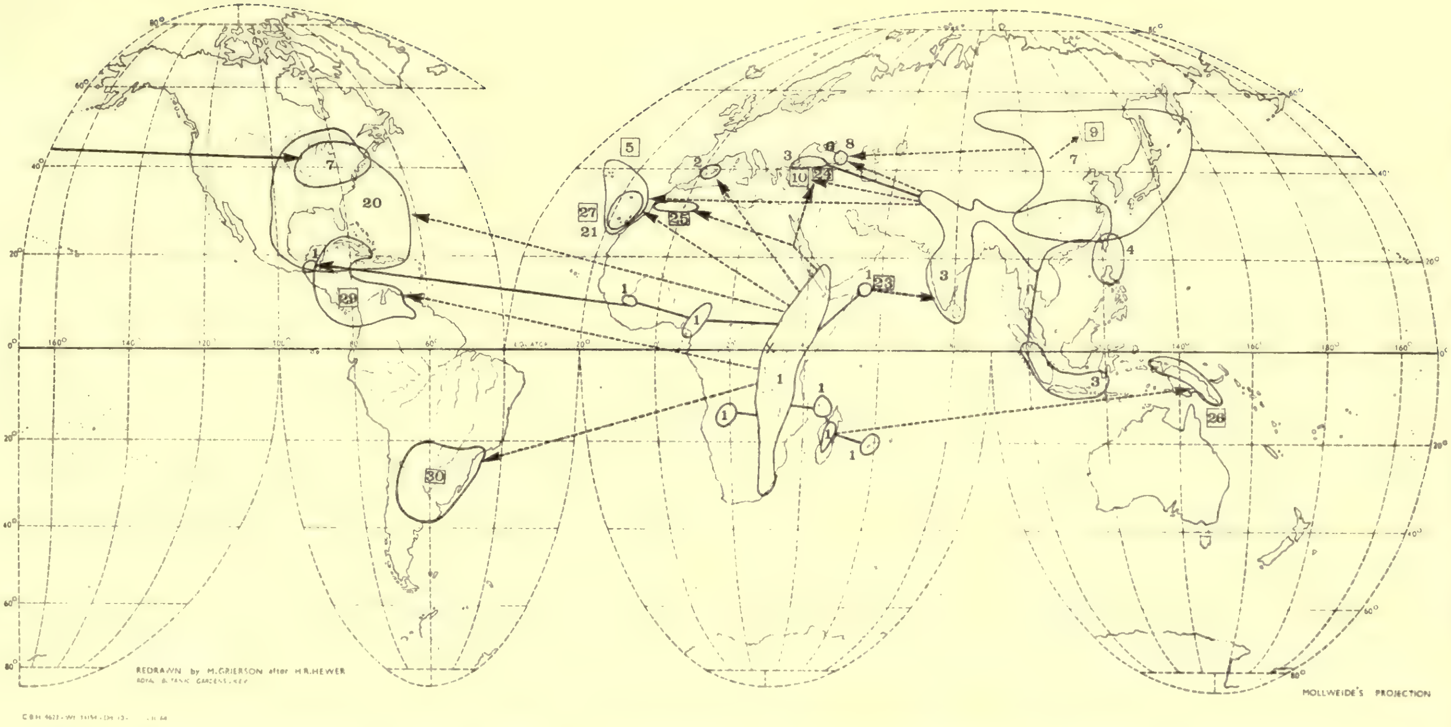

EQUATOR
MOLLWEIDE'S PROJECTION
REDRAWN by M. GRIERSON after H. R. HEWER
ROYAL BOTANIC GARDENS, KEW

FIG. 3. World distribution of *Hypericum*.


5
27
21
25
2
3
10
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8
9
7
20
1
29
30
23
4
26
EQUATOR
REDRAWN by M. GRIERSON after H.R. HEWER
ROYAL BOTANIC GARDENS, KEW
MOLLWEIDE'S PROJECTION

FIG. 4. Distribution of the most primitive section (1. *Campylosporus*) and those immediately related to it and their morphological trends. Sectional numbers in squares denote that only the area of the most primitive species or group of species in the section is indicated, or (sects 9, 10, 24) that the precise area of distribution has not been shown. The area of the most primitive species in the genus (*H. bequaertii* De Wild.) is shown by '×'. Sect. *Campylosporus* does not occur in America as indicated here; see footnote, p. 316.

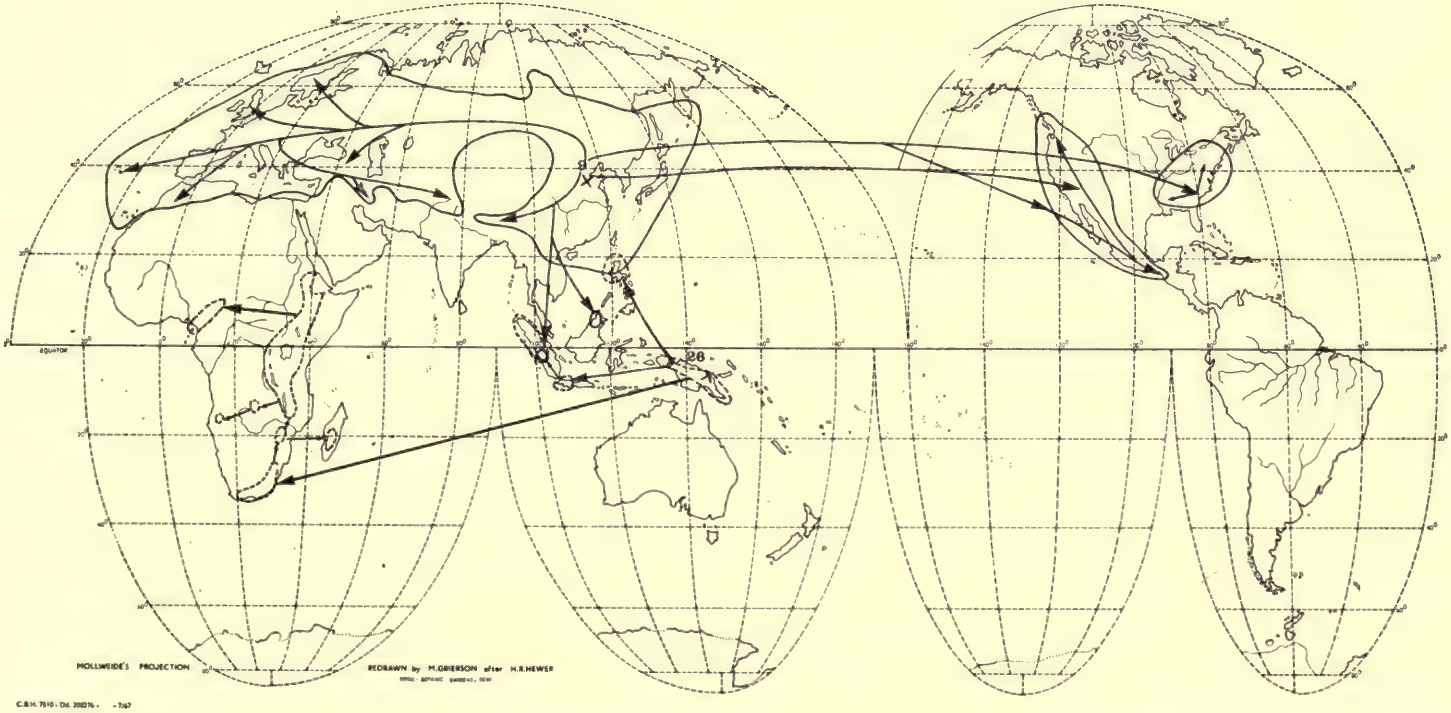
EQUATOR
26
MOLLWEIDE'S PROJECTION
REDRAWN by M.GRIERSON after H.R.HEWER
ROYAL · BOTANIC GARDENS, KEW

FIG. 5. Distribution of sects 9. *Hypericum* and 26. *Humifusoideum* and their morphological trends. Their centres of distribution are each indicated by 'x'.

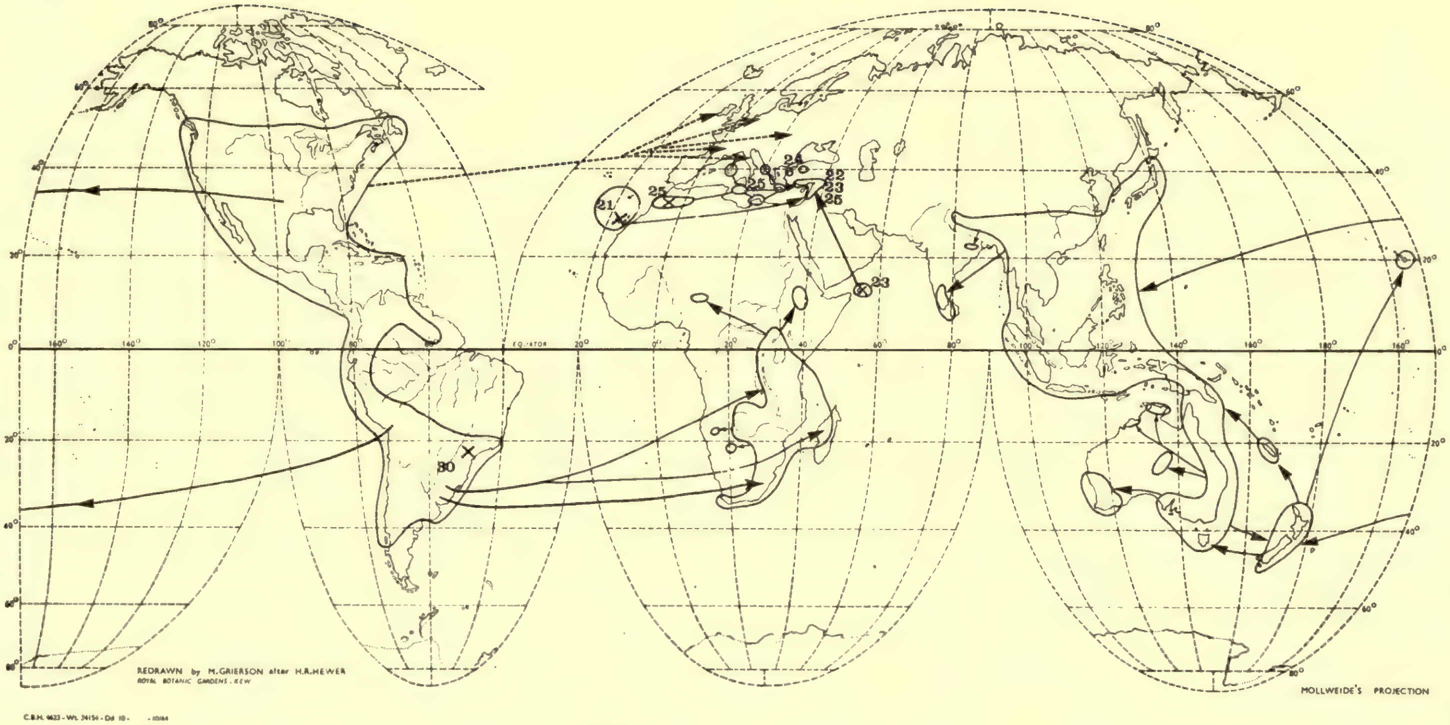
21
22
23
24
25
30
EQUATOR
REDRAWN by M. GRIERSON after H.R. HEWER
ROYAL BOTANIC GARDENS, KEW
MOLLWEIDE'S PROJECTION

FIG. 6. Distribution of sects 21. *Webbia* to 25. *Adenotrias* and 30. *Spachium* and their morphological trends. Their centres of distribution are each indicated by '×', unless their area is small. Interrupted arrows show the occurrence in Europe of N. American species, at least some of which appear to have been introduced there.

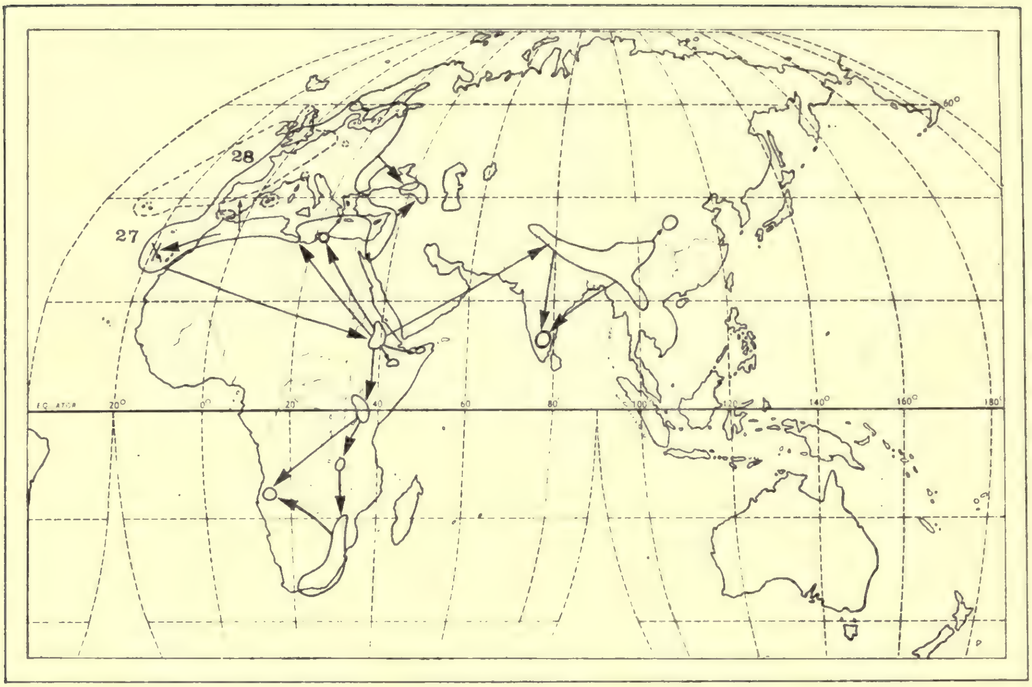
28
27
EQUATOR
20°
0°
20
40
60
80
100
120
140°
160°
180°
60°

FIG. 7. Distribution of sects 27. *Adenosepalum* (——) and 28 *Elodes* (- - - -) and their morphological trends. The areas of the most primitive species in sect. 27 (*H. glandulosum* Ait. and *H. reflexum* L. f.) are indicated by '×'.

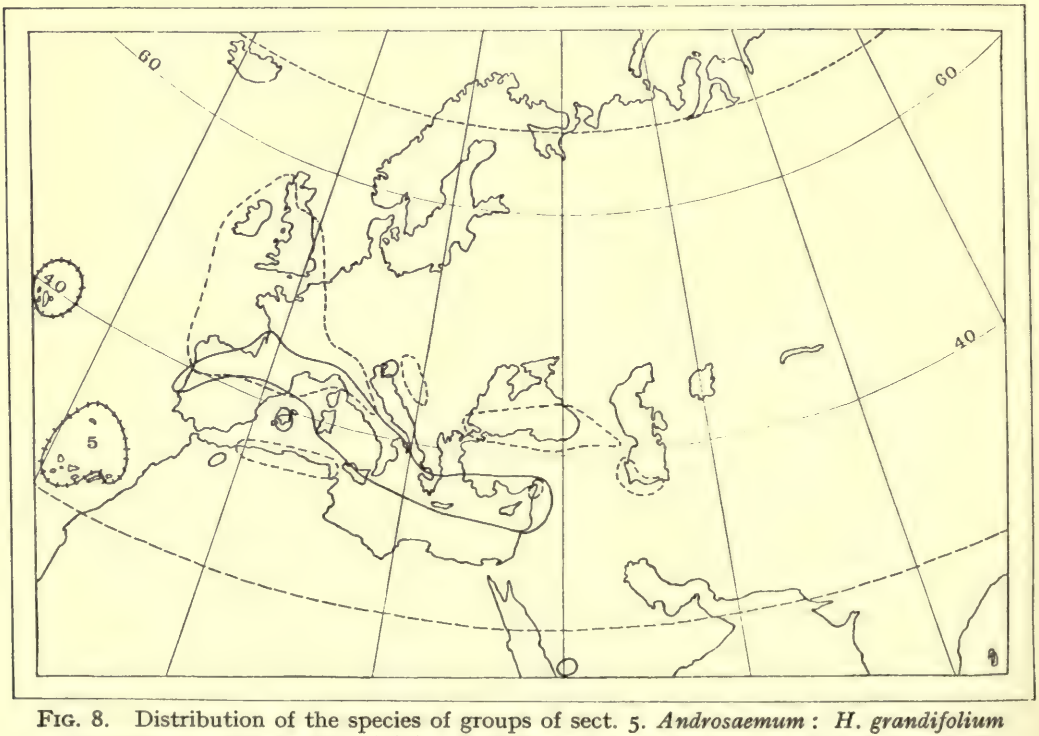

FIG. 8. Distribution of the species of groups of sect. 5. *Androsaemum*: *H. grandifolium* Choisy and *H. foliosum* Ait. (–|–|–|–), *H. hircinum* L. sensu lato (——), *H. androsaemum* L.

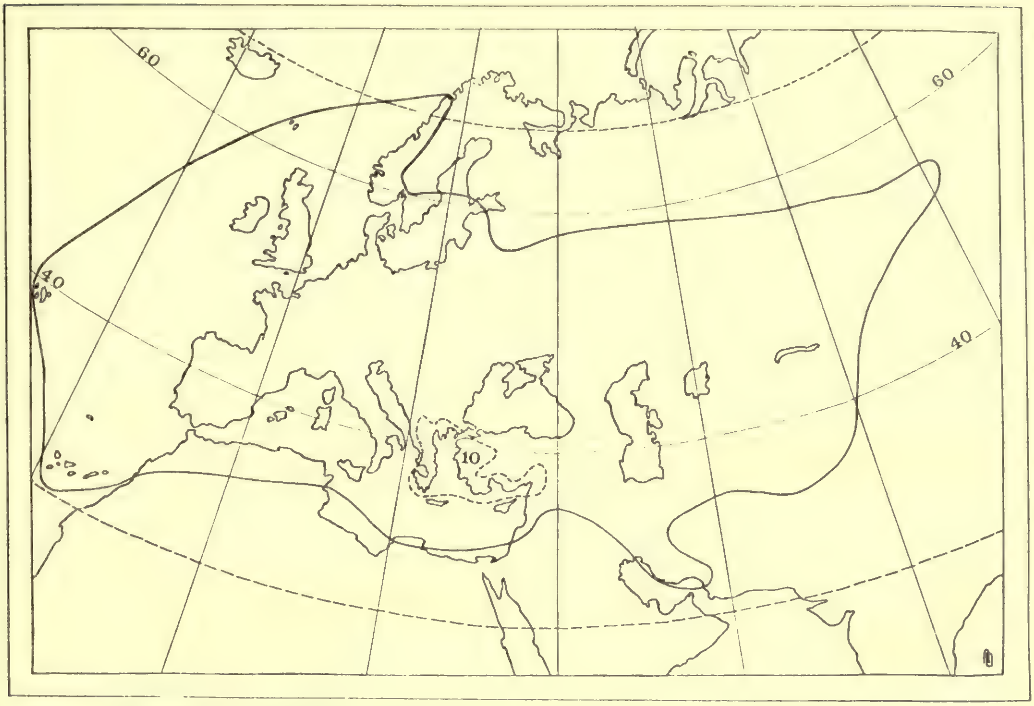

FIG. 9. Distribution of sects 10. *Olympia* to 19. *Coridium* (——) overall and of sect. 10 alone (----).

PROVISIONAL SECTIONAL CLASSIFICATION OF *HYPERICUM*

The sections recognized are listed below, together with their type species and their synonymy, and also an indication of the species that they contain, their geographical distribution, and the basic chromosome numbers and ploidy that have been recorded. Synonyms are entered under the section to which their type species belongs and also elsewhere if their original circumscription included species now placed in other sections. Type species are indicated for taxonomic synonyms. No synonymy is given under the generic name, since all the generic synonyms are quoted under one or other of the sectional names.

All the subdivisions of the genus considered here are treated as sections, but future work may well result in some changes in rank. For example, Sections 10–19 (*Olympia* group) may best be regarded as subsections of a single section; on the other hand, it may be necessary to recognize subsections in Sections 9 (*Hypericum*) or 27 (*Adenosepalum*), both of which are large and variable. Adams (1962) has already proposed a division of the enlarged Section 20 (*Myriandra*) into subsections; these will be considered in a later paper.

Notes on nomenclature

Although this treatment is described as provisional, in the sense that the author considers that further studies in the genus may cause him to modify details of it, all the sectional taxa recognized below are accepted by him, and the new combinations proposed are not provisional names but validly published ones.

In preparing the synonymies that follow, a decision had to be made on a point where the application of the rules was uncertain. Boissier in the *Flora Orientalis* reduced certain previously published sections whose epithets had the form of substantives to the rank of subsection and at the same time altered their epithets into plural adjectives, e.g. *Hypericum* sect. *Milleporum* Spach was called by him *Hypericum* sect. *Euhypericum* subsect. *Millepora,* and the taxon was attributed to Spach ; there is a diagnosis. Boissier's name can be regarded either as a combination based on Spach's with the epithet misspelled or as a new name at a new rank. The publication either of a new combination or of a new name in the circumstances is in accordance with the rules, even although the sectional epithet is invalid. Here, such names are treated as new combinations with misspelled epithets.

HYPERICUM L.

HYPERICUM L., Sp. Pl. : 783 (1753) ; Gen. Pl., ed. 5 : 341 (1754). – Necker, Delic. Gallo-Belg. : 318 (1768) '*Hipericum*'. – J. F. Gmelin in L., Syst. Nat., ed. 13, 2 : 1156 (1791) '*Hypericon*'.

Sect. 1. ***CAMPYLOSPORUS*** (Spach) R. Keller

HYPERICUM sect. CAMPYLOSPORUS (Spach) R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6) : 209 (1893) ; op. cit., ed. 2, 21 : 176 (1925).

Hypericum sect. *Ascyreia* Choisy, Prodr. Monogr. Hypér. : 37, 38 (1821) ; in DC., Prodr. 1 : 544 (1824) pro parte, quoad *H. lanceolatum* Lam., *H. angustifolium* Lam.

Hypericum sect. *Brathys* (Mutis ex L. f.) Choisy, op cit. : 38, 58 (1821) ; in DC., tom. cit. : 553 (1824) pro parte, quoad *H. revolutum* Vahl.

Campylosporus Spach, Hist. Nat. Vég., Phan. 5 : 423 (1836) ; in Annls Sci. nat., sér. 2, Bot. 5 : 363 (1836). Type : *C. reticulatus* Spach, *nom. superfl.* (≡*Hypericum lanceolatum* Lam.) ; lectotype, see Y. Kimura in Nakai & Honda, Nova Fl. Jap. 10 : 112 (1951).

Hypericum B. *Androsaemineae* h. *Campylosporus* (Spach) Endl., Gen. Pl. : 1033 (1840), *status ignot.*

Norysca sensu Blume, Mus. Bot. Lugd. Bat. 2 : 21 (1856) pro parte, quoad *N. lanceolata* (Lam.) Blume, *N. angustifolia* (Lam.) Blume, *N. madagascariensis* (Spach) Blume, non Spach.

Hypericum sect. *Norysca* R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6) : 209 (1893) ; op. cit., ed. 2, 21 : 176 (1925) pro parte, quoad *H. gnidiifolium* A. Rich., non *Norysca* Spach.

Type : *H. lanceolatum* Lam.

Distribution : Tropical and S.E. Africa, Socotra, Yemen, Arabia (Asir), Madagascar, Comoro Is., Réunion, Guatemala*, Mexico*.

10 *species* : *H. bequaertii* De Wild., *H. revolutum* Vahl (incl. *H. Keniense* Schweinf), *H. lanceolatum* Lam., *H. madagascariensis* (Spach) Steudel, *H. roeperanum* W. G. Schimper ex A. Rich., *H. quartinianum* A. Rich., *H. gnidiifolium* A. Rich., *H. synstylum* N. Robson, *H. socotranum* Good, *H. steyermarkii* Standley*.

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* Further studies indicate that *H. steyermarkii,* from Guatemala and Mexico, constitutes a genus separate from *Hypericum.*

Basic chromosome number : unknown.*

Sect. 2. ***PSOROPHYTUM*** (Spach) Nyman

HYPERICUM sect. PSOROPHYTUM (Spach) Nyman, Consp. Fl. Eur. : 132 (1878).

Ascyrum Miller, Gard. Dict. Abridg., ed. 4, 1 (1754) pro parte, quoad sp. 2, non *Ascyrum* L. (1753).

Hypericum sect. *Ascyreia* Choisy, Prodr. Monogr. Hypér. : 37, 38 (1821) ; in DC., Prodr. 1 : 544 (1824) pro parte, quoad *H. balearicum* L.

Psorophytum Spach, Hist. Nat. Vég., Phan. 5 : 413 (1836) ; in Annls Sci. nat., sér. 2, Bot. 5 : 360 (1836). Type : *P. undulatum* Spach, *nom. superfl.* (≡*Hypericum balearicum* L.) ; holotype.

Hypericum B. *Androsaemineae* e. *Psorophytum* (Spach) Endl., Gen. Pl. : 1033 (1840), *status ignot.*

Type : *H. balearicum* L.

Distribution : Balearic Islands.

1 *species* : *H. balearicum* L.

Basic chromosome number : 12 (Nilsson & Lassen, 1971) ; ploidy 2×.

Sect. 3. ***ASCYREIA*** Choisy

HYPERICUM sect. ASCYREIA Choisy, Prodr. Monogr. Hypér. : 37, 38 (1821) ; in DC., Prodr. 1 : 544 (1824) excl. § 1 (Styli vulgo 3) et *H. alternifolium* Vahl, *H. pyramidatum* Aiton, *H. ascyron* L., *H. ascyroides* Willd., *H. rostratum* Raf., *H. lanceolatum* Lam., *H. angustifolium* Lam., *H. kalmianum* L., *H. balearicum* L. Type : *H. calycinum* L. ; lectotype.

Ascyrum Miller, Gard. Dict. Abridg., ed. 4, 1 (1754) quoad descr. sp. 1, excl. nom. Bauhin et sp. 2, non *Ascyrum* L. (1753). Type : *H. calycinum* L. ; lectotype.

Komana Adans., Fam. Pl. 2 : 444, 542 (1763). Type : *Hypericum* Miller, Gard. Dict., t. 151, f. 2 (≡*Hypericum monogynum* L.) ; holotype.

Norysca Spach, Hist. Nat. Vég., Phan. 5 : 426 (1836) ; in Annls Sci. nat., sér. 2, Bot. 5 : 363 (1836). Type : *N. chinensis* Spach (≡*H. chinense* L., non *H. chinense* Osb. ≡*H. monogynum* L.) ; lectotype, see Y. Kimura in Nakai & Honda, Nova Fl. Jap. 10 : 97 (1951).

Eremanthe Spach, Hist. Nat. Vég., Phan. 5 : 421 (1836) ; in Annls Sci. nat., sér, 2. Bot. 5 : 363 (1836). Type : *E. calycina* (L.) Spach (≡*Hypericum calycinum* L.) ; holotype.

Komana subgen. *Centena* Raf., Fl. Tellur. 3 : 79 (1837). Type : *H. monogynum* L. ?

Hypericum B. *Androsaemineae* g. *Eremanthe* (Spach) Endl., Gen. Pl. : 1033 (1840), *status ignot.*

Hypericum B. *Androsaemineae* i. *Norysca* (Spach) Endl., loc. cit., *status ignot.*

Norysca sect. *Verae* Blume, Mus. Bot. Lugd. Bat. 2 : 22 (1856). Type : *N. chinensis* (L.) Spach (=*H. monogynum* L.) ; lectotype.

Norysca sect. *Eremanthe* (Spach) Blume, tom. cit. : 23 (1856).

Hypericum sect. *Eremanthe* (Spach) Boiss., Fl. Orient. 1 : 785 (1867).

Hypericum subgen. *Norysca* (Spach) C. Koch, Dendrologie, 1 : 493 (1869) ? ex parte.

Hypericum sect. *Norysca* (Spach) R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6) : 209 (1893) ; op. cit., ed. 2, 21 : 176 (1925) excl. *H. gnidiifolium* A. Rich., *H. formosanum* Maxim.

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* Chromosome data are from Robson & Adams (1968) unless otherwise indicated.

Type : *H. calycinum* L.

Distribution : Turkey and S. Bulgaria, Pakistan, India and Ceylon to E. China, and south to Lombok and Celebes.

36 *species* : including *H. mysurense* Wight & Arn., *H. gaitii* Haines, *H. oblongifolium* Choisy, *H. calycinum* L., *H. griffithii* Hook. f. & Thomson ex Dyer, *H. monogynum* L., *H. prattii* Hemsley, *H. longistylum* Oliver, *H. cordifolium* Choisy, *H. reptans* Hook. f. & Thomson ex Dyer, *H. pachyphyllum* Collett & Hemsley, *H. augustinii* N. Robson, *H. lobbii* N. Robson, *H. gracilipes* Stapf ex C. E. C. Fischer, *H. tenuicaule* Hook. f. & Thomson ex Dyer, *H. uralum* Buch.-Ham. ex D. Don, *H. patulum* Thunb. ex Murray, *H. leschenaultii* Choisy, *H. choisianum* Wall. ex N. Robson, *H. hookeranum* Wight & Arn., *H. kouytchense* H. Lév., *H. wilsonii* N. Robson, *H. stellatum* N. Robson, *H. dyeri* Rehder, *H. pseudohenryi* N. Robson, *H. acmosepalum* N. Robson, *H. beanii* N. Robson, *H. forrestii* N. Robson, *H. bellum* Li.

Basic chromosome number : 12, 11 (Mehra & Sareen, 1969 ; *H. cernuum* Roxb. = *H. oblongifolium* Choisy), 10, 9 (cf. also Thomas, 1970) ; ploidy 2×, 4×.

Sect. 4. ***TAKASAGOYA*** (Y. Kimura) N. Robson

HYPERICUM sect. TAKASAGOYA (Y. Kimura) N. Robson in Blumea 20 : 252 (1973).

Hypericum sect. *Norysca* sensu R. Keller in Engler & Prantl, Natürl. PflFam., ed. 2, 21 : 176 (1925) pro parte, quoad *H. formosanum* Maxim. ('formosum'), non R. Keller (1893).

Takasagoya Y. Kimura in Bot. Mag., Tokyo 50 : 498 (1936). Type : *T. formosana* (Maxim.) Y. Kimura (≡*Hypericum formosanum* Maxim.) ; holotype.

Type : *H. formosanum* Maxim.

Distribution : Taiwan, Philippines (Luzon).

4 *species* : *H. formosanum* Maxim., *H. nakamurai* (Masamune) N. Robson, *H. subalatum* Hayata, *H. geminiflorum* Hemsley.

Basic chromosome number : unknown.

Sect. 5. ***ANDROSAEMUM*** (Duhamel) Godron

HYPERICUM sect. ANDROSAEMUM (Duhamel) Godron in Gren. & Godron, Fl. France 1 : 320 (1847).

Androsaemum Miller, Gard. Dict. Abridg., ed. 4, 1 (1754), *nom. nud.*

Androsaemum Duhamel, Trait. Arb. Arbust. 1 : 53 (1755). Type : *Hypericum androsaemum* L. ; holotype.

Hypericum sect. *Ascyreia* Choisy, Prodr. Monogr. Hypér. : 37, 38 (1821) ; in DC., Prodr. 1 : 544 (1824) pro parte, quoad *H. elatum* Aiton, *H. grandifolium* Choisy, *H. hircinum* L., *H. foliosum* Aiton.

Hypericum B. *Androsaemineae* f. *Androsaemum* (Duhamel) Endl., Gen. Pl. : 1033 (1840), *status ignot.*, excl. *H. inodorum* Willd.

Hypericum subgen. *Androsaemum* (Duhamel) C. Koch, Dendrologie 1 : 497 (1869), ? ex parte.

Hypericum sect. *Androsaemum* subsect. *Euandrosaemum* R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6) : 211 (1893) ; op. cit., ed. 2, 21 : 177 (1925). Type : *H. androsaemum* L. ; holotype.

Hypericum sect. *Androsaemum* subsect. *Pseudandrosaemum* R. Keller, op. cit. 3 (6) : 211 (1893) ; op. cit., ed. 2, 21 : 177 (1925) excl. *H. concinnum* Benth., *H. inodorum* Willd. Type : *H. hircinum* L. ; lectotype.

Hypericum sect. *Webbia* R. Keller, op. cit. 3 (6) : 211 (1893) ; op. cit., ed. 2, 21 : 177 (1925) pro parte, quoad *H. cambessedesii* Coss. ex Marès & Virgineix, non *Webbia* Spach.

Hypericum sect. *Siciliana* Bubani, Fl. Pyrenaea 3 : 343 (1901) *nom. nud.* Type : *H. bacciforme* Bubani (≡*H. androsaemum* L.) ; holotype.

Hypericum sect. *Pseudandrosaemum* (R. Keller) Stef. in God. Agr.-les. Fak. Univ. Sofiya 11 : 143 (1933) ('*Pseudoandrosaemum*') excl. *H. concinnum* Benth.

Type : *H. androsaemum* L.

Distribution : Macaronesia, W. Europe, Mediterranean to Iran, Arabia (Asir).

4 *species* : *H. grandifolium* Choisy, *H. foliosum* Aiton, *H. hircinum* L., *H. androsaemum* L.

Basic chromosome number : 10 ; ploidy 4×.

Sect. 6. ***INODORA*** Stef.

HYPERICUM sect. INODORA Stef. in God. Agr.-les. Fak. Univ. Sofiya 11 : 147 (1933) '*Inodorum*'. Type : *H. inodorum* Willd. non *H. inodorum* Miller (≡*H. xylosteifolium* (Spach) N. Robson) ; holotype.

Hypericum sect. *Ascyreia* Choisy, Prodr. Monogr. Hypér. : 37, 38 (1821) ; in DC., Prodr. 1 : 544 (1824) pro parte, quoad *H. inodorum* Willd.

Androsaemum sensu Spach, Hist. Nat. Vég., Phan. 5 : 414 (1836) ; in Annls Sci. nat., sér. 2, Bot. 5 : 360 (1836) pro parte, quoad *A. xylosteifolium* Spach, non Duhamel.

Hypericum B. *Androsaemineae* f. *Androsaemum* Endl., Gen. Pl. : 1033 (1840), *status ignot.*, pro parte, quoad *H. inodorum* Willd., non *Androsaemum* Duhamel.

Hypericum sect. *Androsaemum* sensu Boiss., Fl. Orient. 1 : 785 (1867) pro parte, quoad *H. inodorum* Willd.

Hypericum sect. *Androsaemum* subsect. *Pseudandrosaemum* R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6) : 211 (1893) ; op. cit., ed. 2, 21 : 177 (1925) pro parte, quoad *H. inodorum* Willd.

Type : *H. xylosteifolium* (Spach) N. Robson.

Distribution : South-eastern Pontic region (Turkey, U.S.S.R.).

1 *species* : *H. xylosteifolium* (Spach) N. Robson (*H. inodorum* Willd. non *H. inodorum* Miller).

Basic chromosome number : 10, ploidy 4×.

Sect. 7. ***ROSCYNA*** (Spach) R. Keller

HYPERICUM sect. ROSCYNA (Spach) R. Keller in Engl. & Prantl, Natürl. PflFam. 3 (6) : 211 (1893) ; op. cit., ed. 2, 21 : 176 (1925).

Hypericum sect. *Ascyreia* Choisy, Prodr. Monogr. Hypér. : 37, 38 (1821) ; in DC., Prodr. 1 : 544 (1824) pro parte, quoad *H. ascyroides* Willd., *H. pyramidatum* Aiton, *H. ascyron* L.

Ascyrum sensu Poiret in Lam., Tabl. Encycl. Méth., Bot. 3 : 199, t. 642, f. 3 (1823) pro parte, quoad *A. sibiricum* Poiret, non L.

Roscyna Spach, Hist. Nat. Vég., Phan. 5 : 429 (1836) ; in Annls Sci. nat., sér. 2, Bot. 5 : 364 (1836). Type : *R. gmelinii* Spach, *nom. superfl.* (≡*Hypericum ascyron* L.) ; lectotype, see Y. Kimura in Nakai & Honda, Nova Fl. Jap. 10 : 118 (1951).

Hypericum B. *Androsaemineae* k. *Roscyna* (Spach) Endl., Gen. Pl. : 1033 (1840), *status ignot.*

Hypericum subgen. *Roscyna* (Spach) Turczj. in Bull. Soc. Nat. Moscow, 15 : 620 (1842) '*Roseyna*' ? ex parte.

Type : *H. ascyron* L.

Distribution : Altai to Yunnan and Japan ; N.E. America.

3–4 *species* : *H. elatoides* R. Keller, *H. przewalskii* Maxim., *H. ascyron* L. ; also *H. pedunculatum* R. Keller ?

Basic chromosome number : 9 ; ploidy 2×.

Sect. 8. ***BUPLEUROIDES*** Stef.

HYPERICUM sect. BUPLEUROIDES Stef. in God. Agr.-les. Fak. Univ. Sofiya 11 : 160 (1933). Type : *H. bupleuroides* Griseb. ; holotype.

Hypericum sect. *Euhypericum* subsect. *Taeniocarpium* sensu Boiss., Fl. Orient. 1 : 787 (1867) '*Taeniocarpia*' pro parte, quoad *H. bupleuroides* Griseb., non *Hypericum* sect. *Taeniocarpium* Jaub. & Spach.

Hypericum sect. *Euhypericum* subsect. *Homotaenium* R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6) : 212 (1893) ; op. cit., ed. 2, 21 : 178 (1925) pro parte, quoad *H. bupleuroides* Griseb.

Hypericum sect. *Euhypericum* subsect. *Homotaenium* series *Bupleuroidea* Gorschk. in Shishkin & Bobrov, Fl. U.S.S.R. 15 : 246 (1949), *sine descr. lat.*

Type : *H. bupleuroides* Griseb.

Distribution : South-eastern Pontic region (Turkey, U.S.S.R.).

1 *species* : *H. bupleuroides* Griseb.

Basic chromosome number : unknown.

Sect. 9. ***HYPERICUM***

HYPERICUM sect. HYPERICUM, sectio typicum generis.

Hypericum sect. *Perforaria* Choisy, Prodr. Monogr. Hypér. : 37, 44 (1821) ; in DC., Prodr. 1 : 546 (1824) excl. parte, quoad *H. micranthum* Choisy, *H. punctatum* Lam., *H. quadrangulum* L., *H. attenuatum* Choisy, *H. erectum* Thunb., *H. crispum* L., *H. afrum* Lam., *H. perforatum* L., *H. kohlianum* Sprengel, *H. elegans* Stephan ex Willd. Type : *H. perforatum* L. ; lectotype.

Hypericum sect. *Holosepalum* Spach in Annls Sci. nat., sér. 2, Bot. 5 : 357 (1836) excl. parte, quoad *H. crispum* L., *H. quadrangulum* L., *H. tetrapterum* Fries, *H. undulatum* Schousboe ex Willd., *H. punctatum* Lam. Type : *H. tetrapterum* Fries ; lectotype.

Hypericum sect. *Milleporum* Spach, loc. cit. (1836). Type : *H. perforatum* L. ; holotype.

Hypericum sect. *Adenosepalum* Spach, loc. cit. (1836) pro parte, quoad *H. elegans* Stephan ex Willd., *H. formosum* Kunth.

Hypericum A. *Hyperineae* b. *Hypericum* α *Holosepalum* (Spach) Endl., Gen. Pl. : 1032 (1840), *status ignot.*, excl. *H. humifusum* L., *H. nanum* Poiret, *H. cuneatum* Poiret, *H. heterophyllum* Vent.

Hypericum A. *Hyperineae* b. *Hypericum* β *Milleporum* (Spach) Endl., loc. cit. (1840), *status ignot.*

Hypericum A. *Hyperineae* b. *Hypericum* γ *Adenosepalum* Endl., loc. cit. (1840), *status ignot.*, pro parte, quoad *H. elegans* Stephan ex Willd., *H. formosum* Kunth, non *Hypericum* sect. *Adenosepalum* Spach.

Hypericum sect. *Taeniocarpium* Jaub. & Spach, Ill. Pl. Orient. 1 : 47 (1842) pro parte, quoad *H. anagallidioides* Jaub. & Spach, *H. elegans* Stephan ex Willd.

Hypericum sect. *Euhypericum* Godron in Gren. & Godron, Fl. France, 1 : 314 (1847), *nom. invalid.*, excl. parte, quoad *H. perforatum* L., *H. quadrangulum* L., *H. tetrapterum* Fries, *H. corsicum* Steudel. Type : *H. perforatum* L. ; lectotype.

Hypericum sect. *Euhypericum* subsect. *Taeniocarpium* (Jaub. & Spach) Boiss., Fl. Orient. 1 : 787 (1867) '*Taeniocarpia*' pro parte, quoad *H. elegans* Stephan ex Willd., *H. tetrapterum* Fries, *H. crispum* L., non *Hypericum* sect. *Taeniocarpium*, Jaub. & Spach. – Nyman, Consp. Fl. Eur. 1 : 132 (1878) '*Hypericum*' pro nom. sect., pro parte, quoad *H. elegans* Stephan ex Willd., *H. undulatum* Schousboe ex Willd., *H. tetrapterum* Fries, *H. quadrangulum* L., *H. perforatum* L., *H. crispum* L.

Hypericum sect. *Euhypericum* subsect. *Milleporum* (Spach) Boiss., loc. cit. '*Millepora*' excl. parte, quoad *H. perforatum* L.

Holosepalum (Spach) Fourr. in Annls Soc. linn. Lyon, nouv. sér. 16 : 352 (1868) excl. *H. humifusum* (L.) Fourr.

Hypericum sect. *Androsaemum* subsect. *Pseudandrosaemum* R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6) : 211 (1893) ; op. cit., ed. 2, 21 : 177 (1925) pro parte, quoad *H. concinnum* Benth.

Hypericum sect. *Euhypericum* subsect. *Homotaenium* R. Keller, op. cit. 3 (6) : 212 (1893) ; op. cit., ed. 2, 21 : 178 (1925) pro parte, quoad *H. afrum* Lam., *H. attenuatum* Choisy, *H. quadrangulum* L. *H. tetrapterum* Fries, *H. crispum* L., *H. corymbosum* Michaux, *H. scouleri* Hook., *H. elegans* Stephan ex Willd., *H. boeticum* Boiss., *H. undulatum* Schousboe ex Willd., *H. formosum* Kunth, *H. procumbens* R. Keller, non Michaux, *H. petiolulatum* Hook f. & Thoms. ('*petiolatum*'), *H. pseudopetiolatum* R. Keller, *H. faberi* R. Keller ex Hand.-Mazz., *H. oaxacum* R. Keller, *H. seleri* R. Keller, *H. desetangsii* Lamotte, *H. acutum* Moench, *H. erectum* Thunb., *H. mutiloides* R. Keller, *H. mororanense* R. Keller ('*morarense*'), *H. otaruense* R. Keller, *H. wichurae* R. Keller, *H. kamtschaticum* Ledeb., *H. graveolens* Buckley, *H. simulans* Rose, *H. hakonense* Franchet & Savat.

Hypericum sect. *Euhypericum* subsect. *Heterotaenium* R. Keller, op. cit. 3 (6) : 213 (1893) ; op. cit., ed. 2, 21 : 180 (1925) excl. parte, quoad *H. perforatum* L., *H. noeanum* Boiss. Type : *H. perforatum* L. ; lectotype.

Hypericum sect. *Caulopteron* Acloque, Fl. France : 173 (1894) excl. *H. ciliatum* Lam., *H. humifusum* L. Type : *H. perforatum* L. ; lectotype.

Hypericum sect. *Euhypericum* subsect. *Drosocarpium* sensu R. Keller, op. cit., ed. 2, 21 : 180 (1925) pro parte, quoad *H. oshimaense* R. Keller, *H. electrocarpum* Maxim., *H. sampsonii* Hance, non Boiss.

Hypericum sect. *Brathys* subsect. *Eubrathys* sensu R. Keller, tom. cit. : 181 (1925) pro parte, quoad *H. epigeium* R. Keller, non R. Keller (1893).

Hypericum sect. *Brathys* subsect. *Spachium* sensu R. Keller, tom. cit. : 181 (1925) pro parte, quoad *H. collinum* Schlecht. & Cham., non R. Keller (1893).

Hypericum sect. *Pseudandrosaemum* Stef. in God. Agr.-les. Fak. Univ. Sofiya 11 : 143 (1933) '*Pseudoandrosaemum*' pro parte, quoad *H. concinnum* Benth., non *Hypericum* subsect. *Pseudandrosaemum* R. Keller.

Hypericum sect. *Perforata* Stef., tom. cit. : 174 (1933) excl. *H. tomentosum* L., *H. lusitanicum* Poiret, *H. pubescens* Boiss. Type : *H. perforatum* L. ; lectotype.

Hypericum sect. *Euhypericum* subsect. *Drosocarpium* sensu Y. Kimura in Bot. Mag. Tokyo 54 : 86 (1940) pro parte, quoad *H. sampsonii* Hance, non R. Keller.

Hypericum sect. *Euhypericum* subsect. *Homotaenium* series *Attenuata* Gorschk. in Shishkin & Bobrov, Fl. U.S.S.R. 15 : 236 (1949), *sine descr. lat.*

Hypericum sect. *Euhypericum* subsect. *Homotaenium* series *Kamtschatica* Gorschk., tom. cit. : 237 (1949), *sine descr. lat.*

Hypericum sect. *Euhypericum* subsect. *Homotaenium* series *Acuta* Gorschk., tom. cit. : 241 (1949), *sine descr. lat.*

Hypericum sect. *Euhypericum* subsect. *Homotaenium* series *Quadrangula* Gorschk., tom. cit. : 242 (1949), *sine descr. lat.*

Hypericum sect. *Euhypericum* subsect. *Homotaenium* series *Elegantia* Gorschk., tom. cit. : 243 (1949), *sine descr. lat.*

Hypericum sect. *Euhypericum* subsect. *Homotaenium* series *Crispa* Gorschk., tom. cit. : 244 (1949), *sine descr. lat.*

Hypericum sect. *Euhypericum* subsect. *Heterotaenium* series *Perforata* Gorschk., tom. cit. : 247 (1949), *sine descr. lat.*

Hypericum sect. *Drosocarpium* sensu Y. Kimura in Nakai & Honda, Nova Fl. Jap 10 : 127 (1951) pro parte, quoad *H. sampsonii* Hance, non Spach.

Hypericum sect. *Homotaenium* Y. Kimura, tom. cit. : 135 (1951) pro parte, non *Hypericum* subsect. *Homotaenium* R. Keller.*

Hypericum sect. *Homotaenium* series *Quadrangula* Y. Kimura, tom. cit. : 136 (1951). Type : *H. quadrangulum* L., *nom. ambig.* (= *H. tetrapterum* Fries) ; holotype.

Hypericum sect. *Homotaenium* series *Crispa* Y. Kimura, loc. cit. (1951). Type : *H. crispum* L. (= *H. triquetrifolium* Turra) ; holotype.

Hypericum sect. *Homotaenium* series *Bilineata* Y. Kimura, loc. cit. (1951) et greges. Type : *H. attenuatum* Choisy ; holotype.

Hypericum sect. *Homotaenium* series *Elineata* Y. Kimura, loc. cit. (1951) et greges. Type : *H. erectum* Thunb. ex Murray.

Hypericum sect. *Pulogensia* N. Robson in Blumea 20 : 259 (1973) pro parte, quoad spp. Taiwanianae.

Type : *H. perforatum* L.

Distribution : North temperate zone and southward to Guatemala, the Sudan Republic (? introduced), Sabah and Sumatra. *H. perforatum* L. introduced into several other parts of the world.

About 48 *species* : including *H. concinnum* Benth., *H. maculatum* Crantz, *H. tetrapterum* Fries, *H. undulatum* Schousboe ex Willd., *H. afrum* Lam., *H. perforatum* L., *H. triquetrifolium* Turra, *H. attenuatum* Choisy, *H. elegans* Stephan ex Willd., *H. yezoense* Maxim., *H. tosaense* Makino, *H. nagasawai* Hayata, *H. taiwanianum* Y. Kimura, *H. nokoense* Ohwi ; *H. yamamotoi* Miyabe & Y. Kimura, *H. samaniense* Miyabe & Y. Kimura, *H. oliganthum* Franchet & Savat., *H. ovalifolium* Koidz., *H. kamtschaticum* Ledeb., *H. hakonense* Franchet & Savat., *H. sikokumontanum* Makino, *H. kiusianum* Koidz., *H. penthorodes* Koidz., *H. yakusimense* Koidz., *H. vulcanicum* Koidz., *H. erectum* Thunb. ex Murray, *H. kinashianum* Koidz., *H. seniawinii* Maxim., *H. faberi* R. Keller ex Hand.-Mazz., *H. petiolulatum* Hook. f. & Thomson ex Dyer, *H. pseudopetiolatum* R. Keller, *H. sampsonii* Hance, *H. graveolens* Buckley, *H. mitchellianum* Rydb., *H. punctatum* Lam., *H. pseudomaculatum* Bush, *H. seleri* R. Keller, *H. scouleri* Hook., *H. formosum* Kunth, *H. oaxacum* R. Keller, *H. epigeium* R. Keller, *H. collinum* Schlecht. & Cham.

Basic chromosome number : 9 (Hsu, 1968), 8, 7 ; ploidy 2 ×, 4 ×, 5 ×, 6 ×.

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* Y. Kimura cites *H. erectum* Thunb. as the type of this section, but this species was not included by R. Keller (1893) in his subsection.

Sect. 10. ***OLYMPIA*** (Spach) Nyman

Hypericum sect. Olympia (Spach) Nyman, Consp. Fl. Eur. : 132 (1878) excl. *H. apollinis* Boiss. & Heldr.

Hypericum sect. *Ascyreia* Choisy, Prodr. Monogr. Hypér. : 37 (1821) ; in DC., Prodr. 1 : 544 (1824) pro parte, quoad *H. olympicum* L.
Olympia Spach, Hist. Nat. Vég., Phan. 5 : 406 (1836) ; in Annls Sci. nat., sér. 2, Bot. 5 : 359 (1836). Type : *O. glauca* Spach, *nom. superfl.* (≡*Hypericum olympicum* L.) ; holotype.
Hypericum A. *Hyperineae* c. *Olympia* (Spach) Endl., Gen. Pl. : 1033 (1840), *status ignot.*
Hypericum sect. *Euhypericum* subsect. *Olympia* (Spach) Boiss., Fl. Orient. 1 : 786 (1867), excl. *H. apollinis* Boiss. & Heldr.

Type : *H. olympicum* L.

Distribution : South Balkan Peninsula, western Turkey ; Caucasus ?

2 *species* : *H. olympicum* L., *H. polyphyllum* Boiss. & Balansa.

Basic chromosome number : 9 ; ploidy 2×.

Sect. 11. ***CAMPYLOPUS*** Boiss.

Hypericum sect. Campylopus Boiss., Fl. Orient. 1 : 785 (1867).

Campylopus Spach, Hist. Nat. Vég., Phan. 5 : 411 (1836) ; in Annls Sci. nat., sér. 2, Bot. 5 : 360 (1836), non *Campylopus* Brid. (1819). Type : *C. cerastoides* Spach (≡*Hypericum cerastoides* (Spach) N. Robson =*H. rhodoppeum* Frivald.) ; holotype.
Campylopelma Reichenb., Handb. Nat. Pflanzensyst. : 307 (1837) ≡*Campylopus* Spach non Brid.
Hypericum B. *Androsaemineae* d. *Campylopus* Endl., Gen. Pl. : 1033 (1840), *status ignot.*

Type : *H. cerastoides* (Spach) N. Robson.

Distribution : North-eastern Aegean region.

1 *species* : *H. cerastoides* (Spach) N. Robson.

Basic chromosome number : 8 ; ploidy 2×.

Sect. 12. ***ORIGANIFOLIA*** Stef.

Hypericum sect. Origanifolia Stef. in God. Agr.-les. Fak. Univ. Sofiya 11 : 166 (1933) excl. *H. trichocaulon* Boiss. & Heldr. Type : *H. origanifolium* Willd., lectotype.

Hypericum sect. *Perforaria* Choisy, Prodr. Monogr. Hypér. : 37, 44 (1821) ; in DC., Prodr. 1 : 546 (1824) pro parte, quoad *H. origanifolium* Willd.
Hypericum sect. *Taeniocarpium* Jaub. & Spach, Ill. Pl. Orient. 1 : 47 (1842) pro parte, quoad *H. aviculariifolium* Jaub. & Spach.
Hypericum sect. *Drosocarpium* sensu Jaub. & Spach, tom. cit. : 35 (1842) pro parte, quoad *H. origanifolium* Willd., non Spach.
Hypericum sect. *Euhypericum* subsect. *Milleporum* Boiss., Fl. Orient. 1 : 787 (1867) '*Millepora*' pro parte, excl. *H. perforatum* L., *H. ciliatum* Lam., non *Hypericum* sect. *Milleporum* Spach.
Hypericum sect. *Euhypericum* subsect. *Heterotaenium* R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6) : 213 (1893) ; op. cit., ed. 2, 21 : 180 (1925) pro parte, excl. *H. perforatum* L., *H. ciliatum* Lam.

Hypericum sect. *Uniflora* Stef., tom. cit. : 168 (1933). Type : *H. uniflorum* Boiss. & Heldr. (≡*H. aviculariifolium* subsp. *uniflorum* (Boiss. & Heldr.) N. Robson) ; holotype.

Hypericum sect. *Euhypericum* subsect. *Heterotaenium* series *Origanifolia* Gorschk. in Shishkin & Bobrov, Fl. U.R.S.S. 15 : 247 (1949), *sine descr. lat.*

Type : *H. origanifolium* Willd.

Distribution : Turkey, U.S.S.R. (Georgia).

4 *species* : *H. origanifolium* Willd., *H. aviculariifolium* Jaub. & Spach, *H. salsugineum* Robson & Huber-Mor., *H. imbricatum* Poulter.

Basic chromosome number : 9 ; ploidy 2×.

Sect. 13. ***DROSOCARPIUM*** Spach

HYPERICUM sect. DROSOCARPIUM Spach in Annls Sci. nat., sér. 2, Bot. 5 : 358 (1836). Type : *H. barbatum* Jacq. ; lectotype, see Y. Kimura in Nakai & Honda, Nova Fl. Jap. 10 : 127 (1951).

Ascyrum Miller, Gard. Dict. abridg., ed. 4, 1 (1754) pro parte, quoad *A. magno flore* C.B.P., excl. descr., non *Ascyrum* L. (1753).

Hypericum sect. *Perforaria* Choisy, Prodr. Monogr. Hypér. : 37, 44 (1821) ; in DC., Prodr. 1 : 546 (1824) pro parte, quoad *H. barbatum* Jacq., *H. dentatum* Loisel., *H. fimbriatum* Lam., *H. ciliatum* Lam.

Hypericum A. *Hyperineae* δ *Drosocarpium* (Spach) Endl., Gen. Pl. : 1033 (1840), *status ignot.*

Hypericum sect. *Euhypericum* Godron in Gren. & Godron, Fl. France 1 : 314 (1847), *nom. invalid.*, pro parte, quoad *H. richeri* Vill., *H. burseri* DC., *H. ciliatum* Lam.

Hypericum sect. *Euhypericum* subsect. *Olympia* Boiss., Fl. Orient. 1 : 786 (1867) pro parte, quoad *H. apollinis* Boiss. & Heldr., non *Olympia* Spach.

Hypericum sect. *Euhypericum* subsect. *Milleporum* Boiss., tom. cit. : 787 (1867) '*Millepora*', pro parte, quoad *H. ciliatum* Lam., *H. trichocaulon* Boiss. & Heldr., non *Hypericum* sect. *Milleporum* Spach.

Hypericum sect. *Euhypericum* subsect. *Drosocarpium* (Spach) Boiss., tom. cit. : 788 (1867) '*Drosocarpia*' – Nyman, Consp. Fl. Eur. : 132 (1878) '*Hypericum*' pro nom. sect.

Drosocarpium (Spach) Fourr. in Annls Soc. linn. Lyon, nouv. sér. 16 : 353 (1868). – R. Keller in Engler & Prantl, Natürl. PflFam. ed. 2, 21 : 180 (1925) excl. *H. oshimaense* R. Keller, *H. electrocarpum* Maxim., *H. sampsonii* Hance.

Hypericum sect. *Euhypericum* subsect. *Taeniocarpium* sensu Nyman, loc. cit. (1878) '*Taeniocarpia*', '*Hypericum*' pro nom. sect., pro parte, quoad *H. perfoliatum* L., *H. trichocaulon* Boiss. & Heldr., non Boiss.

Hypericum sect. *Euhypericum* subsect. *Heterotaenium* R. Keller, op. cit. 3 (6) : 213 (1893) ; op. cit., ed. 2, 21 : 180 (1925) pro parte, quoad *H. ciliatum* Lam., *H. boissieri* Petrović, *H. trichocaulon* Boiss. & Heldr.

Hypericum sect. *Kelleria* Stef. in God. Agr.-les. Fak. Univ. Sofiya 11 : 161 (1933). Type : *H. kelleri* Baldacci ; holotype.

Hypericum sect. *Origanifolia* Stef., tom. cit. : 166 (1933) pro parte, quoad *H. trichocaulon* Boiss. & Heldr.

Hypericum sect. *Euhypericum* subsect. *Drosocarpium* series *Nordmanniana* Gorschk. in Shishkin & Bobrov, Fl. U.R.S.S. 15 : 253 (1949), *sine descr. lat.*

Hypericum sect. *Euhypericum* subsect. *Drosocarpium* series *Caucasica* Gorschk., tom. cit. : 254 (1949), *sine descr. lat.*

Type : *H. barbatum* Jacq.

Distribution: Madeira, Mediterranean region, Pyrenees, Alps, Balkans, Levant, Pontus, U.S.S.R. (Georgia).

About 12 *species*: *H. vesiculosum* Griseb., *H. perfoliatum* L., *H. montbretii* Spach, *H. umbellatum* A. Kerner, *H. bithynicum* Boiss., *H. richeri* Vill., *H. spruneri* Boiss., *H. rochelii* Griseb. & Schenk, *H. barbatum* Jacq., *H. rumeliacum* Boiss., *H. trichocaulon* Boiss. & Heldr., *H. kelleri* Baldacci; also *H. setiferum* Stef.?

Basic chromosome numbers: 8 (Contandriopoulos & Lanzalavi, 1968), 7; ploidy 2×, 4×.

Sect. 14. *OLIGOSTEMA* (Boiss.) Stef.

HYPERICUM sect. OLIGOSTEMA (Boiss.) Stef. in God. Agr.-les. Fak. Univ. Sofiya 11: 158 (1933).

Hypericum sect. *Perforaria* Choisy, Prodr. Monogr. Hypér.: 37, 44 (1821); in DC., Prodr. 1: 546 (1824) pro parte, quoad *H. repens*. L., *H. humifusum* L., *H. linarifolium* Vahl.

Hypericum sect. *Holosepalum* Spach in Annls Sci. nat., sér. 2, Bot. 5: 357 (1836) pro parte, quoad *H. humifusum* L.

Hypericum sect. *Adenosepalum* Spach, loc. cit. (1836) pro parte, quoad *H. linarifolium* Vahl '*linearifolium*'.

Hypericum A. *Hyperineae* b. *Hypericum* α *Holosepalum* Endl., Gen. Pl.: 1032 (1840), *status ignot.*, pro parte, quoad *H. humifusum* L., non *Hypericum* sect. *Holosepalum Spach.*

Hypericum A. *Hyperineae* b. *Hypericum* γ *Adenosepalum* Endl., loc. cit. (1840), *status ignot.*, pro parte, quoad *H. linarifolium* '*linearifolium*', non *Hypericum* sect. *Adenosepalum* Spach.

Hypericum sect. *Taeniocarpium* Jaub. & Spach, Ill. Pl. Orient. 1: 47 (1842) pro parte, quoad *H. linarifolium* Vahl '*linearifolium*', *H. australe* Ten., *H. aucheri* Jaub. & Spach.

Hypericum sect. *Euhypericum* Godron in Gren. & Godron, Fl. France 1: 314 (1847), *nom. invalid.*, pro parte, quoad *H. humifusum* L.

Hypericum sect. *Euhypericum* subsect. *Oligostema* Boiss., Fl. Orient. 1: 786 (1867). – Nyman, Consp. Fl. Eur.: 134 (1878) '*Oligostemata*', '*Hypericum*' pro nom. sect. Type: *H. humifusum* L.; holotype.

Hypericum sect. *Euhypericum* subsect. *Taeniocarpium* Boiss., tom. cit.: 787 (1867) '*Taeniocarpia*', pro parte, quoad *H. aucheri* Jaub. & Spach, non *Hypericum* sect. *Taeniocarpium* Jaub. & Spach. – Nyman, op cit.: 132 (1878) '*Hypericum*' pro nom. sect., pro parte, quoad *H. australe* Ten.

Holosepalum Fourr. in Annls Soc. linn. Lyon, nouv. sér. 16: 352 (1868) pro parte. quoad *H. humifusum* (L.) Fourr., non *Hypericum* sect. *Holosepalum* Spach.

Hypericum sect. *Hypericum* subsect. *Coridium* sensu Nyman. op. cit.: 134 (1878) '*Coridia*' pro parte, quoad *H. linarifolium* Vahl, non Boiss.

Hypericum sect. *Euhypericum* subsect. *Homotaenium* R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6): 212 (1893); op. cit., ed. 2, 21: 178 (1925) pro parte, quoad *H. australe* Ten., *H. linarifolium* Vahl '*linearifolium*', *H. tenellum* Janka.

Hypericum sect. *Acaulopteron* Acloque, Fl. France: 173 (1894) pro parte, quoad *H. australe* Ten., *H. linarifolium* Vahl.

Hypericum sect. *Caulopteron* Acloque, loc. cit. (1894) pro parte, quoad *H. humifusum* L.

Hypericum sect. *Euhypericum* subsect. *Triadenioides* sensu R. Keller, op. cit., ed. 2, 21: 178 (1925) pro parte, quoad *H. modestum* Boiss., non Boiss.

Hypericum sect. *Modesta* Stef., tom. cit.: 161 (1933). Type: *H. modestum* Boiss.; holotype.

Hypericum sect. *Montana* Stef., tom. cit.: 162 (1933) pro parte, quoad *H. linarifolium* Vahl, *H. australe* Ten., *H. aucheri* Jaub. & Spach.

Hypericum sect. *Euhypericum* subsect. *Oligostema* series *Humifusa* Gorschk. in Shishkin & Bobrov, Fl. U.R.S.S. 15: 219 (1949), *sine descr. lat.*, excl. parte, quoad *H. humifusum* L.

Type : *H. humifusum* L.

Distribution : Macaronesia, Europe, Mediterranean region.

7 species : *H. aucheri* Jaub. & Spach, *H. repens* L., *H. australe* Ten., *H. linarifolium* Vahl, *H. humifusum* L., *H. andjerinum* Font Quer & Pau, *H. modestum* Boiss.

Basic chromosome number : 8 ; ploidy 2×.

Sect. 15. *THASIA* Boiss.

HYPERICUM sect. THASIA Boiss., Fl. Orient. 1 : 785 (1867). – R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6) : 209 (1893) ; op. cit., ed. 2, 21 : 176 (1925) '*Thasium*'. Type : *H. thasium* Griseb. ; holotype.

Type : *H. thasium* Griseb.

Distribution : South-eastern Balkan Peninsula, Thasos.

1 species : *H. thasium* Griseb.

Basic chromosome number : unknown.

Sect. 16. *CROSSOPHYLLUM* Spach

HYPERICUM sect. CROSSOPHYLLUM Spach in Annls Sci. nat., sér. 2, Bot. 5 : 359 (1836). Type : *H. ptarmicifolium* Spach, '*ptarmicaefolium*' (≡ *H. orientale* L.) ; lectotype.

Hypericum sect. *Perforaria* Choisy, Prodr. Monogr. Hypér. : 37, 44 (1821) ; in DC., Prodr. 1 : 546 (1842) pro parte, quoad *H. orientale* L.

Hypericum A. *Hyperineae* b. *Hypericum* ζ *Crossophyllum* (Spach) Endl., Gen. Pl. : 1033 (1840), *status ignot.*

Hypericum sect. *Euhypericum* subsect. *Crossophyllum* (Spach) Boiss., Fl. Orient. 1 : 786 (1867) '*Crossophylla*'.

Hypericum sect. *Euhypericum* subsect. *Crossophyllum* series *Ptarmicifolia* Gorschk. in Shishkin & Bobrov, Fl. U.R.S.S. 15 : 222 (1949), *sine descr. lat.*

Type : *H. orientale* L.

Distribution : North and west Turkey, Caucasus.

2 species : *H. orientale* L., *H. adenotrichum* Spach.

Basic chromosome number : 8 ; ploidy 2×.

Sect. 17. *HIRTELLA* Stef.

HYPERICUM sect. HIRTELLA Stef. in God. Agr.-les. Fak. Univ. Sofiya 11 : 183 (1933). Type : *H. hirtellum* (Spach) Boiss. ; lectotype.

Hypericum sect. *Perforaria* Choisy, Prodr. Monogr. Hypér. : 37, 44 (1821) ; in DC., Prodr. 1 : 546 (1824) pro parte, quoad *H. hyssopifolium* Vill. (excl. var. *pauciglandulosum* Choisy ?), *H. capitatum* Choisy, *H. scabrum* L., *H. triplinerve* Vent.

Eremosporus Spach, Hist. Nat. Vég., Phan. 5 : 374 (1836) ; in Annls Sci. nat., sér. 2, Bot. 5 : 355 (1836). Type : *E. olivieri* Spach (≡*Hypericum olivieri* (Spach) Boiss.) ; holotype.

Drosanthe Spach, Hist. Nat. Vég., Phan. 5 : 376 (1836) ; in Annls Sci. nat., sér. 2, Bot. 5 : 355 (1836). Type : *D. hirtella* Spach (≡*Hypericum hirtellum* (Spach) Boiss.) ; lectotype, see Y. Kimura in Nakai & Honda, Nova Fl. Jap. 10 : 113 (1951).

Hypericum sect. *Adenosepalum* Spach in Annls Sci. nat., sér. 2, Bot. 5 : 357 (1836) pro parte, quoad *H. hyssopifolium* Vill., *H. triplinerve* Vent.

Hypericum a. *Drosanthineae* a. *Eremosporus* (Spach) Endl., Gen. Pl. : 1032 (1840), *status ignot.*

Hypericum a. *Drosanthineae* b. *Drosanthe* (Spach) Endl., loc. cit. (1840), *status ignot.*

Hypericum A. *Hyperineae* b. *Hypericum* γ *Adenosepalum* Endl., loc. cit. (1840), *status ignot.*, pro parte, quoad *H. hyssopifolium* Vill., *H. triplinerve* Vent., non *Hypericum* sect. *Adenosepalum* Spach.

Hypericum sect. *Taeniocarpium* Jaub. & Spach, Ill. Pl. Orient. 1 : 47 (1842) pro parte, quoad *H. hyssopifolium* Vill. var. *hyssopifolium*, *H. retusum* Aucher-Eloy ex Jaub. & Spach, *H. asperulum* Jaub. & Spach.

Thymopsis Jaub. & Spach, tom. cit. : 72 (1842). Type : *T. aspera* Jaub. & Spach (≡*Hypericum thymopsis* Boiss.) ; holotype.

Hypericum sect. *Euhypericum* Godron in Gren. & Godron, Fl. France 1 : 314 (1847), *nom invalid.*, pro parte, quoad *H. hyssopifolium* Vill.

Hypericum sect. *Euhypericum* subsect. *Taeniocarpium* (Jaub. & Spach) Boiss., Fl. Orient. 1 : 787 (1867) '*Taeniocarpia*' pro parte, quoad *H. scabrum* L., *H. laeve* Boiss. & Hausskn., *H. thymopsis* Boiss., *H. hirtellum* (Spach) Boiss., *H. assyriacum* Boiss., *H. hyssopifolium* Vill., *H. callianthum* Boiss. & Noé, *H. helianthemoides* (Spach) Boiss., *H. adenocladum* Boiss., *H. olivieri* (Spach) Boiss., *H. leptocladum* Boiss., *H. retusum* Aucher, *H. amanum* Boiss., *H. spectabile* Jaub. & Spach, non *Hypericum* sect. *Taeniocarpium* Jaub. & Spach – Nyman, Consp. Fl. Eur. : 132 (1878) '*Hypericum*' pro nom. sect., pro parte, quoad *H. hyssopifolium* Vill.

Hypericum sect. *Euhypericum* subsect. *Homotaenium* R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6) : 212 (1893) ; op. cit., ed. 2, 21 : 178 (1925) pro parte, quoad spec. Boiss. supra cit.

Hypericum sect. *Acaulopteron* Acloque, Fl. France : 173 (1894) pro parte, quoad *H. hyssopifolium* Vill.

Hypericum sect. *Pulchra* Stef., tom. cit. : 177 (1933) pro parte, quoad *H. amanum* Boiss., *H. nabelekii* Stef.

Hypericum sect. *Hyssopifolia* Stef., tom. cit. : 178 (1933), excl. *H. hirsutum* L., *H. kotschyanum* Boiss., *H. confertum* Choisy, *H. neurocalycinum* Boiss. & Heldr., *H. pruinatum* Boiss. & Balansa, *H. armenum* Jaub. & Spach, *H. theodorii* Woronow, *H. alpestre* Steven. Type : *H. hyssopifolium* Vill. ; lectotype.

Hypericum sect. *Spectabiles* Stef., tom. cit. : 182 (1933). Type : *H. spectabile* Jaub. & Spach ; lectotype.

Hypericum sect. *Scabra* Stef., tom. cit. : 185 (1933). Type : *H. scabrum* L. ; holotype.

Hypericum sect. *Euhypericum* subsect. *Homotaenium* series *Scabra* Gorschk. in Shishkin & Bobrov, Fl. U.R.S.S. 15 : 224 (1949), *sine descr. lat.*

Hypericum sect. *Euhypericum* subsect. *Homotaenium* series *Pontica* Gorschk., tom. cit. : 228 (1949) *sine descr. lat.*

Hypericum sect. *Euhypericum* subsect. *Homotaenium* series *Helianthemoidea* Gorschk., tom. cit. : 229 (1949), *sine descr. lat.*

Hypericum sect. *Euhypericum* subsect. *Homotaenium* series *Elongata* Gorschk., tom. cit. : 230 (1949), *sine descr. lat.*

Hypericum sect. *Drosanthe* (Spach) Y. Kimura in Nakai & Honda, Nova Fl. Jap. 10 : 113 (1951).

Type : *H. hirtellum* (Spach) Boiss.

Distribution : Mediterranean, Turkey, Crimea, Iraq, Caucasus to Altai Mts.

24 species : including *H. elongatum* Ledeb., *H. apricum* Karelin & Kiril., *H. uniglandulosum* Hausskn. ex Bornm., *H. salsolifolium* Hand.-Mazz., *H. hyssopifolium* Vill., *H. lydium* Boiss., *H. amblysepalum* Hochst., *H. spectabile* Jaub. & Spach, *H. lysimachioides* Boiss. & Noé, *H. asperulum* Jaub. & Spach, *H. hirtellum* (Spach) Boiss., *H. retusum* Aucher-Eloy, *H. libanoticum* N. Robson, *H. pseudolaeve* N. Robson, *H. thymbrifolium* Boiss. & Noé, *H. helianthemoides* (Spach) Boiss., *H. vermiculare* Boiss. & Hausskn., *H. olivieri* (Spach) Boiss., *H. capitatum* Choisy, *H. scabroides* Robson & Poulter, *H. scabrum* L., *H. thymopsis* Boiss.

Basic chromosome number : 8 (Reynaud, 1973) ; ploidy 3× ?*

Sect. 18. ***TAENIOCARPIUM*** Jaub. & Spach

HYPERICUM sect. TAENIOCARPIUM Jaub. & Spach, Ill. Pl. Orient. 1 : 47 (1842) excl. parte, quoad *H. repens* sensu Jaub. & Spach, *H. saturejifolium* Jaub. & Spach, *H. hyssopifolium* var. *hirtellum* Jaub. & Spach. Type : *H. repens* sensu Jaub. & Spach (= *H. linarioides* Bosse) ; lectotype, see N. Robson in Notes R. Bot. Gdn. Edinb. 27 : 194 (1967).

Hypericum sect. *Perforaria* Choisy, Prodr. Monogr. Hypér. : 37, 44 (1821) ; in DC., Prodr. 1 : 546 (1824) pro parte, quoad *H. hirsutum* L., *H. nummularium* L., *H. pulchrum* L., *H. serpyllifolium* Lam., *H. confertum* Choisy.

Hypericum sect. *Adenosepalum* Spach in Annls Sci. nat., sér. 2, Bot. 5 : 357 (1836) pro parte, quoad *H. serpyllifolium* Lam., *H. pulchrum* L., *H. nummularium* L.

Hypericum A. *Hyperineae* b. *Hypericum* γ *Adenosepalum* Endl., Gen. Pl. : 1032 (1840), *status ignot.*, pro parte, quoad *H. serpyllifolium* Lam., *H. pulchrum* L., *H. nummularium* L., non *Hypericum* sect. *Adenosepalum* Spach.

Hypericum sect. *Helianthemoides* Jaub. & Spach, tom. cit. : 65 (1842). Type : *H. armenum* Jaub. & Spach ; holotype.

Hypericum sect. *Euhypericum* Godron in Gren. & Godron, Fl. France 1 : 314 (1847), *nom. invalid.*, pro parte, quoad *H. pulchrum* L., *H. hirsutum* L., *H. nummularium* L.

Hypericum sect. *Euhypericum* subsect. *Triadenioides* (Jaub. & Spach) Boiss., Fl. Orient. 1 : 786 (1867) '*Triadenioidea*' pro parte, quoad *H. serpyllifolium* Lam., *H. crenulatum* Boiss., *H. fragile* Heldr. & Sart. – Nyman, Consp. Fl. Eur. : 134 (1878) '*Hypericum*' pro nom. sect., pro parte, quoad *H. fragile* Heldr. & Sart. – R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6) : 212 (1895) ; op. cit., ed. 2, 21 : 178 (1925) pro parte, quoad species cit. cum *H. nummularioides* Trautv., H. *nummularium* L.

Hypericum sect. Euhypericum subsect. *Taeniocarpium* (Jaub. & Spach) Boiss., tom. cit. : 787 (1867) '*Taeniocarpia*' excl. parte, quoad *H. confertum* Choisy, *H. neurocalycinum* Boiss., *H. hirsutum* L., *H. repens* sensu Jaub. & Spach, *H. kotschyanum* Boiss., *H. armenum* Jaub. & Spach, *H. venustum* Fenzl. – Nyman, tom. cit. : 132 (1878) '*Hypericum*' pro nom. sect., excl. parte, quoad *H. pulchrum* L., *H. hirsutum* L., *H. repens* sensu Jaub. & Spach.

Adenosepalum Fourr. in Annls Soc. linn. Lyon, nouv. sér. 16 : 352 (1868) pro parte, quoad *A. pulchrum* (L), Fourr., *A. nummularium* (L.) Fourr., *A. hirsutum* (L.) Fourr., non *Hypericum* sect. *Adenosepalum* Spach.

Hypericum sect. *Hypericum* subsect. *Nummularia* Nyman, tom. cit. : 134 (1878), *nom. nud.*

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* In view of the occurrence of only $x=9$, 8 and 7 in adjacent sections, Reynaud's record of $2n=24$ for *H. scabrum* L. is unlikely to represent a diploid number based on $n=12$. Triploidy on $x=8$ is probable but further counts in Sect. *Hirtella* are necessary before tetraploidy on $x=6$ can be discounted.

Hypericum sect. *Euhypericum* subsect. *Homotaenium* R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6) : 212 (1893) ; op. cit., ed. 2, 21 : 178 (1925) excl. parte, quoad *H. confertum* Choisy, *H. hirsutum* L., *H. pruinatum* Boiss. & Balansa, *H. kotschyanum* Boiss., *H. repens* sensu Jaub. & Spach, *H. pulchrum* L., *H. serbicum* Petrov (nomen ?), *H. armenum* Jaub. & Spach. Type : *H. repens* sensu Jaub. & Spach (=*H. linarioides* Bosse) ; lectotype.

Hypericum sect. *Acaulopteron* Acloque, Fl. France : 173 (1894) pro parte, quoad *H. hirsutum* L., *H. pulchrum* L., *H. nummularium* L.

Hypericum sect. *Euhypericum* subsect. *Arthrophyllum* sensu R. Keller, op. cit., ed. 2, 21 : 178 (1925) pro parte, quoad *H. pumilio* Bornm., non Jaub. & Spach.

Hypericum sect. *Serpyllifolium* Stef. in God. Agr.-les. Fak. Univ. Sofiya 11 : 151 (1933). Type : *H. serpyllifolium* Lam. (=*H. thymifolium* Banks & Solander) ; holotype.

Hypericum sect. *Haplophylloides* Stef., tom. cit. : 152 (1933). Type : *H. haplophylloides* Halacsy & Baldacci ; holotype.

Hypericum sect. *Nummularia* Stef., tom. cit. : 153 (1933). Type : *H. nummularium* L. ; lectotype.

Hypericum sect. *Ovalifolia* Stef., tom. cit. : 153 (1933) *'Ovalifolium'*. Type : *H. ovalifolium* Stef. non Koidz. (≡*H. monadenum* N. Robson) ; holotype.

Hypericum sect. *Fragilia* Stef., tom. cit. : 154 (1933). Type : *H. fragile* Heldr. & Sart. ; lectotype.

Hypericum sect. *Pulchra* Stef., tom. cit. : 177 (1933) excl. *H. amanum* Boiss., *H. nabelekii* Stef. Type : *H. pulchrum* L. ; lectotype.

Hypericum sect. *Hyssopifolia* Stef., tom. cit. : 178 (1933) pro parte, quoad *H. hirsutum* L., *H. kotschyanum* Boiss., *H. confertum* Choisy, *H. neurocalycinum* Boiss. & Heldr., *H. pruinatum* Boiss. & Balansa, *H. armenum* Jaub. & Spach, *H. theodorii* Woronow, *H. alpestre* Steven.

Hypericum sect. *Euhypericum* subsect. *Triadenioides 'Triadenioidea'* series *Nummularioidea* Gorschk. in Shishkin & Bobrov, Fl. U.R.S.S. 15 : 221 (1949), *sine descr. lat.*

Hypericum sect. *Euhypericum* subsect. *Homotaenium* series *Hirsuta* Gorschk., tom. cit. : 227 (1949), *sine descr. lat.*

Hypericum sect. *Euhypericum* subsect. *Homotaenium* series *Perplexa* Gorschk., tom. cit. : 232 (1949), *sine descr. lat.*

Hypericum sect. *Euhypericum* subsect. *Homotaenium* series *Armena* Gorschk., tom. cit. : 235 (1949), *sine descr. lat.*

Hypericum sect. *Euhypericum* subsect. *Homotaenium* series *Montana* Gorschk., tom. cit. : 245 (1949), *sine descr. lat.*, pro parte, quoad *H. venustum* Fenzl.

Hypericum sect. *Homotaenium* (R. Keller) Y. Kimura in Nakai & Honda, Nova Fl. Jap. 10 : 135 (1951) quoad series *Hirsuta* Y. Kimura pro parte et series *Adenosepala* Y. Kimura pro parte*.

Hypericum sect. *Homotaenium* series *Hirsuta* Y. Kimura, tom. cit. : 136 (1951) excl. parte, quoad typum. Type : *H. hirsutum* L., holotype.

Hypericum sect. *Homotaenium* series *Adenosepala* Y. Kimura, loc. cit. (1951) pro parte, excl. *H. montanum* L.

Type : *H. linarioides* Bosse.

Distribution : Europe, Mediterranean, Turkey, Caucasus, Iran, Kazakhstan (?).

22–23 *species* : *H. hirsutum* L., *H. confertum* Choisy, *H. pruinatum* Boiss. & Balansa, *H. kotschyanum* Boiss., *H. neurocalycinum* Boiss. & Heldr., *H. venustum* Fenzl, *H. pulchrum* L., *H. fursei* N. Robson, *H. linarioides* Bosse, *H. armenum* Jaub. & Spach, *H. theodorii* Woronow, *H. fissurale* Woronow, *H. crenulatum* Boiss., *H. nummularioides* Trautv., *H. nummularium* L., *H. monadenum* N. Robson, *H.*

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* The type cited by Kimura, *H. erectum* Thunb., was not included by Keller (1893) in his *Hypericum* subsect. *Homotaenium*, but Kimura cites this as the basionym of his section.

pumilio Bornm., *H. fragile* Heldr. & Sart., *H. saxifragum* Robson & Huber-Mor., *H. taygeteum* Quezel & Contandr., *H. thymifolium* Banks & Solander, *H. haplophylloides* Halacsy & Baldacci ; also *H. eleanorae* Jelenev. ?

Basic chromosome number : 9 ; ploidy 2×.

Sect. 19. ***CORIDIUM*** Spach

HYPERICUM sect. CORIDIUM Spach in Annls Sci. nat., sér. 2, Bot. 5 : 358 (1836). Type : *H. coris* L. ; lectotype, see Stefanoff in God. Agr.-les. Fak. Univ. Sofiya 11 : 156 (1933).

Hypericum sect. *Perforaria* Choisy, Prodr. Monogr. Hypér. : 37, 44 (1821) ; in DC., Prodr. 1 : 546 (1824) pro parte, quoad *H. empetrifolium* Willd., *H. coris* L., *H. ericoides* L.

Hypericum A. *Hyperineae* b. *Hypericum* ε *Coridium* (Spach) Endl., Gen. Pl. : 1033 (1840), *status ignot.*

Hypericum sect. *Euhypericum* Godron in Gren. & Godron, Fl. France 1 : 314 (1847), *nom. invalid.*, pro parte, quoad *H. coris* L.

Hypericum sect. *Euhypericum* subsect. *Coridium* (Spach) Boiss., Fl. Orient. 1 : 786 (1867) '*Coridia*'. – Nyman, Consp. Fl. Eur. : 134 (1878) '*Hypericum*' pro nom. sect., excl. *H. linarifolium* Vahl, *H. lusitanicum* Poiret. – R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6) : 211 (1893) ; op. cit., ed. 2, 21 : 177 (1925).

Hypericum sect. *Acaulopteron* Acloque, Fl. France : 173 (1894) pro parte, quoad *H. coris* L.

Hypericum sect. *Empetrifolia* Stef., tom. cit. : 149 (1933). Type : *H. empetrifolium* Willd. ; lectotype.

Hypericum sect. *Ericoides* Stef., tom. cit. : 150 (1933). Type : *H. ericoides* L. ; lectotype.

Hypericum sect. *Galiifolia* Stef., tom. cit. : 156 (1933). Type : *H. asperuloides* Czernj. (= *H. galiifolium* Rupr.) ; holotype.

Hypericum sect. *Euhypericum* subsect. *Coridium* series *Asperuloidea* Gorschk. in Shishkin & Bobrov, Fl. U.R.S.S. 15 : 218 (1949), *sine descr. lat.*

Type : *H. coris* L.

Distribution : Southern Spain, N.W. Africa, Alps, Balkans and Aegean region, Caucasus.

5 *species* : *H. empetrifolium* Willd., *H. amblycalyx* Coust. & Gandoger, *H. coris* L., *H. asperuloides* Czernj. ex Turcz., *H. ericoides* L.

Basic chromosome number : 9 ; ploidy 2×.

Sect. 20. ***MYRIANDRA*** (Spach) R. Keller

HYPERICUM sect. MYRIANDRA (Spach) R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6) : 214 (1893) ; op. cit., ed. 2, 21 : 180 (1925).

Ascyrum L., Sp. Pl. : 787 (1753) ; Gen. Pl., ed. 5 : 342 (1754) excl. *A. villosum* L. et *A. crux-andreae* L. pro parte, quoad syn. – Engler in Engler & Prantl, Natürl. PflFam. 3 (6) : 208 (1893) ; op. cit., ed. 2, 21 : 174 (1925) pro parte, excl. *A. filicaule* Dyer. Type : *A. hypericoides* L (= *Hypericum hypericoides* (L.) Crantz) ; lectotype, see Britton & Brown, Ill. Fl. N. Un. States, ed. 2, 2 : 528 (1913).

Hypericoides Adans., Fam. Pl. 2 : 443, 616 (1763). Type : *Ascyrum hypericoides* L. ; lectotype.

Hypericum sect. *Ascyreia* Choisy, Prodr. Monogr. Hypér. : 37, 38 (1821) ; in DC., Prodr. 1 : 544 (1824) pro parte, quoad *H. frondosum* Michaux, *H. amoenum* Pursh, *H. kalmianum* L.

Hypericum sect. *Perforaria* Choisy, op. cit. 37, 44 (1821) ; in DC., tom. cit. : 546 (1824) pro parte, quoad *H. dolabriforme* Vent., *H. cistifolium* Lam., *H. densiflorum* Pursh, *H. procumbens* Michaux, *H. rosmarinifolium* Lam., *H. prolificum* L., *H. glaucum* Michaux, *H. nudiflorum* Michaux, *H. sphaerocarpum* Michaux, *H. galioides* Lam., *H. axillare* Lam.

Hypericum sect. *Brathys* Choisy, op. cit. : 38, 58 (1821) ; in DC., tom. cit. : 553 (1824) pro parte, quoad *H. axillare* Lam., *H. nitidum* Lam., *H. fasciculatum* Lam., non *Brathys* Mutis ex L. f.

Myriandra Spach, Hist. Nat. Vég., Phan. 5 : 434 (1836) ; in Annls Sci. nat., sér. 2, Bot. 5 : 364 (1836). Type : *M. prolifica* (L.) Spach (≡*Hypericum prolificum* L.) ; lectotype, see Y. Kimura in Nakai & Honda, Nova Fl. Jap. 10 : 23 (1951).

Brathydium Spach, Hist. Nat. Vég., Phan. 5 : 442 (1836) ; in Annls Sci. nat., sér. 2, Bot. 5 : 365 (1836). Type : *B. grandiflorum* Spach, *nom. superfl.* (≡*Hypericum dolabriforme* Vent.) ; lectotype, see Y. Kimura, tom. cit. : 24 (1951) (as *B. dolabriforme* (Vent.) Y. Kimura).

Isophyllum Spach, Hist. Nat. Vég., Phan. 5 : 432 (1836) ; in Annls Sci. nat., sér. 2, Bot. 5 : 367 (1836), non *Isophyllum* Hoffmann (1814). Type : *I. drummondii* Spach (=*Hypericum microsepalum* (Torrey & Gray) A. Gray ex S. Watson) ; holotype.

Streptalon Raf., Fl. Tellur. 3 : 80 (1837). Type : *S. dolabriforme* (Vent.) Raf. (≡*Hypericum dolabriforme* Vent.) ; holotype.

Ascyrum b. *Isophyllum* (Spach) Endl., Gen. Pl. : 1032 (1840) *status ignot.*

Hypericum C. *Brathydineae* l. *Myriandra* (Spach) Endl., tom. cit. : 1033 (1840), *status ignot.*

Hypericum C. *Brathydineae* m. *Brathydium* (Spach) Endl., tom. cit. : 1033 (1840), *status ignot.*

Hypericum subgen. *Myriandra* (Spach) C. Koch, Dendrologie, 1 : 499 (1869) ? excl. parte.

Hypericum sect. *Myriandra* subsect. *Centrosperma* R. Keller, op. cit. 3 (6) : 214 (1893) ; op. cit., ed. 2, 21 : 180 (1925). Type : *H. prolificum* L. ; lectotype, see P. Adams in Contr. Gray Herb. Harv. 189 : 12 (1962).

Hypericum sect. *Myriandra* subsect. *Suturosperma* R. Keller, op. cit. 3 (6) : 214 (1893) ; op. cit., ed. 2, 21 : 180 (1925). Type : *H. nudiflorum* Michaux, lectotype.

Hypericum sect. *Brathydium* (Spach) R. Keller, op. cit. 3 (6) : 214 (1893) ; op. cit., ed. 2, 21 : 181 (1925).

Hypericum sect. *Brathydium* subsect. *Eubrathydium* R. Keller, op. cit. 3 (6) : 214 (1893), *nom. invalid.* ; op. cit., ed. 2, 21 : 181 (1925). Type : *H. dolabriforme* Vent. ; lectotype.

Hypericum sect. *Brathydium* subsect. *Pseudobrathydium* R. Keller, op. cit. 3 (6) : 214 (1893) ; op. cit., ed. 2, 21 : 181 (1925). – P. Adams, tom. cit. : 35 (1962) sub sect. *Myriandra.* Type : *H. buckleyi* M. A. Curtis ; holotype.

Crookea Small, Fl. Southeastern U.S. : 786, 1335 (1903). Type : *C. microsepala* (Torrey & Gray) Small (≡*Hypericum microsepalum* (Torrey & Gray) A. Gray ex S. Watson) ; holotype.

Hypericum sect. *Brathys* subsect. *Eubrathys* R. Keller, op. cit., ed. 2, 21 : 181 (1925), *nom. invalid.*, pro parte, quoad *H. nitidum* Lam.

Hypericum sect. *Brathys* subsect. *Spachium* R. Keller, op. cit., ed. 2, 21 : 181 (1925) pro parte, quoad *H. adpressum* W. Barton ('Bast.').

Hypericum sect. *Myriandra* subsect. *Brathydium* (Spach) P. Adams, tom. cit. : 36 (1962), *nom. synon.*

Hypericum sect. *Isophyllum* (Spach) P. Adams, tom. cit. : 36 (1962), *nom. synon.*

Type : *H. prolificum* L.

Distribution : Eastern and central N. America, Central America south to Honduras Republic, Bermuda, Bahamas, Greater Antilles.

30 *species* : *H. kalmianum* L., *H. lobocarpum* Gattinger, *H. densiflorum* Pursh, *H. prolificum* L., *H. frondosum* Michaux, *H. galioides* Lam., *H. lissophloeus* P.

Adams, *H. chapmanii* P. Adams, *H. fasciculatum* Lam., *H. nitidum* Lam., *H. brachyphyllum* (Spach) Steudel, *H. reductum* P. Adams, *H. lloydii* (Svenson) P. Adams, *H. exile* P. Adams, *H. myrtifolium* Lam., *H. nudiflorum* Michaux, *H. apocynifolium* Small, *H. buckleyi* M. A. Curtis, *H. cistifolium* Lam., *H. sphaerocarpum* Michaux, *H. dolabriforme* Vent., *H. adpressum* W. Barton, *H. ellipticum* Hook., *H. microsepalum* (Torrey & Gray) A. Gray ex S. Watson, *H. crux-andreae* (L.) Crantz *H. edisonianum* (Small) Adams & Robson, *H. tetrapetalum* Lam., *H. hypericoides* (L.) Crantz, *H. stragulum* Adams & Robson, *H. suffruticosum* Adams & Robson.

Basic chromosome number: 9; ploidy 2×.

Sect. 21. ***WEBBIA*** (Spach) R. Keller

HYPERICUM sect. WEBBIA (Spach) R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6) : 211 (1893) ; op. cit., ed. 2, 21 : 177 (1925) excl. *H. cambessedesii* Cosson ex Marès & Vigineix.

Hypericum sect. *Ascyreia* Choisy, Prodr. Monogr. Hypér. : 37, 38 (1821) ; in DC., Prodr. 1 : 544 (1824) pro parte, quoad *H. canariense* L., *H. floribundum* Aiton.

Webbia Spach, Hist. Nat. Vég., Phan. 5 : 408 (1836) ; in Annls Sci. nat., sér. 2, Bot. 5 : 356 (1836). Type : *W. platypetala* Spach (≡ *Hypericum canariense* L.) ; lectotype.*

Hypericum A. *Hyperineae* a. *Webbia* (Spach) Endl., Gen. Pl. : (1) 32 (1840), *status ignot.*

Type: *H. canariense* L.

Distribution: Canary Is., Madeira.

1 *species*: *H. canariense* L.

Basic chromosome number: 10, ploidy 4×.

Sect. 22. ***ARTHROPHYLLUM*** Jaub. & Spach

HYPERICUM sect. ARTHROPHYLLUM Jaub. & Spach, Ill. Pl. Orient. 1 : 44 (1842). Type : *H. rupestre* Jaub. & Spach ; lectotype, see Y. Kimura in Nakai & Honda, Nova Fl. Jap. 10 : 113 (1951).

Hypericum sect. *Perforaria* Choisy, Prodr. Monogr. Hypér. : 37, 44 (1821) ; in DC., Prodr. 1 : 546 (1824) pro parte, quoad *H. nanum* Poiret.

Hypericum sect. *Holosepalum* Spach in Annls Sci. nat., sér. 2, Bot. 5 : 357 (1836) pro parte, quoad *H. nanum* Poiret.

Hypericum A. *Hyperineae* b. *Hypericum* α *Holosepalum* (Spach) Endl., Gen. Pl. : 1032 (1840), *status ignot.* pro parte, quoad *H. nanum* Poiret.

Hypericum sect. *Euhypericum* subsect. *Arthrophyllum* (Jaub. & Spach) Boiss., Fl. Orient. 1 : 786 (1867) '*Arthrophylla*' – R. Keller in Engler & Prantl, Natürl. PflFam., ed. 2, 21 : 178 (1925) excl. *H. pumilio* Bornm.

Type: *H. rupestre* Jaub. & Spach.

Distribution: Levant, southern Turkey.

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* Spach (at first) did not include the Linnaean species in his new genus: he merely suggested that *W. heterophylla* or *W. platypetala* might be synonymous with *Hypericum canariense* L.

4 *species* : *H. cardiophyllum* Boiss., *H. rupestre* Jaub. & Spach, *H. nanum* Poiret, *H. vacciniifolium* Hayek & Siehe.

Basic chromosome number : unknown.

Sect. 23. ***TRIADENIOIDES*** Jaub. & Spach

HYPERICUM sect. TRIADENIOIDES Jaub. & Spach, Ill. Pl. Orient. 1 : 49 (1842). – Stef. in God. Agr.-les. Fak. Univ. Sofiya 11 : 145 (1933) '*Triadenioidea*' pro parte, quoad *H. scopulorum* Balf. f. '*scopulosum*'. Type : *H. cuneatum* Poiret (= *H. pallens* Banks & Solander) ; holotype.

Hypericum sect. *Holosepalum* Spach in Annls Sci. nat., sér. 2, Bot. 5 : 357 (1836) pro parte, quoad *H. cuneatum* Poiret.

Hypericum A. *Hyperineae* b. *Hypericum* α *Holosepalum* (Spach) Endl., Gen. Pl. : 1032 (1840), *status ignot.*, pro parte, quoad *H. cuneatum* Poiret.

Hypericum sect. *Euhypericum* subsect. *Triadenioides* (Jaub. & Spach) Boiss., Fl. Orient. 1 : 786 (1867) '*Triadenioidea*' – R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6) : 212 (1893) excl. parte, quoad typum ; op. cit., ed. 2, 21 : 178 (1925) excl. parte, quoad *H. scopulorum* Balf. f. '*scopulosum*', *H. cuneatum* Poiret.

Hypericum sect. *Cuneata* Stef., op. cit. : 151 (1933) '*Cuneatum*' *nom. superfl.* Type : *H. cuneatum* Poiret (= *H. pallens* Banks & Solander) ; holotype.

Type : *H. pallens* Banks & Solander.

Distribution : Socotra, Levant, southern Turkey,

5 *species* : including *H. scopulorum* Balf. f., *H. tortuosum* Balf f., *H. ternatum* Poulter, *H. pallens* Banks & Solander.

Basic chromosome number : 8 (Reynaud, 1973) ; ploidy 2×.

Sect. 24. ***HETEROPHYLLA*** N. Robson

HYPERICUM sect. HETEROPHYLLA N. Robson in Notes R. Bot. Gdn, Edinb. 27 : 185 (1967) '*Heterophyllum*'. Type : *H. heterophyllum* Vent. ; holotype.

Hypericum sect. *Perforaria* Choisy, Prodr. Monogr. Hypér. : 37, 44 (1821) ; in DC., Prodr. 1 : 546 (1824) pro parte, quoad *H. heterophyllum* Vent.

Hypericum sect. *Holosepalum* Spach in Annls Sci. nat., sér. 2, Bot. 5 : 357 (1836) pro parte, quoad *H. heterophyllum* Vent.

Hypericum A. *Hyperineae* b. *Hypericum* α *Holosepalum* (Spach) Endl., Gen. Pl. : 1032 (1840), *status ignot.*, pro parte, quoad *H. heterophyllum* Vent.

Hypericum sect. *Euhypericum* subsect. *Triadenioides* (Jaub. & Spach) Boiss., Fl. Orient. 1 : 786 (1867) '*Triadenioides*', pro parte, quoad *H. heterophyllum* Vent. – R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6) : 212 (1803) ; op. cit., ed. 2, 21 : 178 (1925).

Hypericum sect. *Triadenioides* sensu Stef. in God. Agr.-les. Fak. Univ. Sofiya 11 : 145 (1933) '*Triadenioidea*', pro parte, quoad *H. heterophyllum* Vent., non Jaub. & Spach.

Type : *H. heterophyllum* Vent.

Distribution : North-western Turkey.

1 *species* : *H. heterophyllum* Vent.

Basic chromosome number : 9 (Reynaud, 1973) ; ploidy 2×.

Sect. 25. ***ADENOTRIAS*** (Jaub. & Spach) R. Keller

Hypericum sect. Adenotrias (Jaub. & Spach) R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6) : 209 (1893) ; op. cit., ed. 2, 21 : 175 (1925).

Elodes Adans., Fam. Pl. 2 : 444, 553 (1763) pro parte, quoad '*Hypericum* 9 Lin. Sp. 784'.

Martia Sprengel, Anl. Kennt. Gewächse, ed. 2, 2 : 788 (1818), nom illegit. pro parte, quoad '*Elodea* Adans.' pro parte ; in L., Syst. Veg., ed. 16, 3 : 333 (1826) pro parte, quoad *M. polyandra* Sprengel (≡*Hypericum aegypticum* L.).

Hypericum sect. *Perforaria* Choisy, Prodr. Monogr. Hypér. : 37, 44 (1821) : in DC., Prodr. 1 : 546 (1824) pro parte, quoad *H. aegypticum* L. '*aegyptiacum*'.

Elodea sensu Jack, Malayan Misc. 2 (7) : 25 (1822) ; in Hooker's J. Bot. 1 : 371 (1834) pro parte, quoad *E. aegyptica* (L.) Jack '*Egyptiaca*'.

Triadenia Spach in Annls Sci. nat., sér. 2, Bot. 5 : 172, 354 (1836) ; Hist. Nat. Vég., Phan. 5 : 370 (1836). Type : *T. microphylla* Spach, *nom. superfl.* (≡*Hypericum aegypticum* L.) ; lectotype.

Episiphis Ref., Fl. Tellur. 3 : 78 (1837). Type : *E. parvifolia* Ref., *nom. superfl.* (≡*Hypericum aegypticum* L.) ; holotype.

Elodes c. *Triadenia* (Spach) Endl., Gen. Pl. : 1034 (1840) '*Elodea*', *status ignot.*

Adenotrias Jaub. & Spach, Ill. Pl. Orient. 1 : 76 (1842). Type : *A. phrygia* Jaub. & Spach (≡*Hypericum* russeggeri (Fenzl) R. Keller) ; lectotype.

Elodes d. *Adenotrias* (Jaub. & Spach) Endl., Gen. Pl., Suppl. 5 : 70 (1850) '*Elodea*', *status ignot.*

Triadenia sect. *Eutriadenia* Boiss., Fl. Orient. 1 : 783 (1867) *nom. invalid.* Type : *T. aegyptica* (L.) Boiss. '*aegyptiaca*' (≡*Hypericum aegypticum* L.) ; lectotype.

Triadenia sect. *Adenotrias* (Jaub. & Spach) Boiss., tom. cit. : 784 (1867).

Hypericum sect. *Triadenia* (Spach) R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6) : 208 (1893) ; op. cit., ed. 2, 21 : 175 (1925).

Elodes sect. *Adenotrias* (Jaub. & Spach) Y. Kimura in Nakai & Honda, Nova Fl. Jap. 10 : 18 (1951). – Greuter in Candollea 20 : 216 (1965).

Type : *Hypericum russeggeri* Fenzl.

Distribution : Morocco to the Levant.

3 *species* : *H. russeggeri* Fenzl, *H. aciferum* (Greuter) N. Robson, *H. aegypticum* L.

Basic chromosome number : 10 (Ornduff, pers. comm.).

Sect. 26. ***HUMIFUSOIDEUM*** R. Keller

Hypericum sect. Humifusoideum R. Keller in Engler & Prantl, Natürl. PlFam. 3 (6) : 211 (1893) ; op. cit., ed. 2, 21 : 177 (1925). – N. Robson in Kew Bull. 12 : 436 (1958), excl. *H. kiboense* Oliv., *H. conjunctum* N. Robson non *H. conjunctum* Y. Kimura, *H. aethiopicum* Thunb. ; in Blumea 20 : 257 (1973). Type : *H. peplidifolium* A. Rich. ; holotype.

Hypericum sect. *Euhypericum* subsect. *Homotaenium* sensu R. Keller in Engler & Prantl, Natürl. PflFam., ed. 2, 21 : 178 (1925) pro parte, quoad *H. hellwigii* Lauterb., *H. wilmsii* R. Keller, non R. Keller (1893).

Hypericum sect. *Brathys* subsect. *Spachium* sensu R. Keller, op cit., ed. 2, 21 : 181 (1925) pro parte, quoad *H. woodii* R. Keller, non R. Keller (1893).

Hypericum sect. *Pulogensia* N. Robson in Blumea 20 : 259 (1973) excl. spp. Taiwanianae. Type : *H. pulogense* Merr. ; holotype.

Type : *H. peplidifolium* A. Rich.

Distribution : Tropical and South Africa, Madagascar, New Guinea, Philippines, Java, Sumatra.

10 *species* : *H. sewense* N. Robson, *H. macgregorii* F. v. Muell., *H. saruwagedicum* Diels, *H. bifurcatum* N. Robson, *H. papuanum* Ridley, *H. natalense* J. M. Wood & Evans, *H. wilmsii* R. Keller, *H. peplidifolium* A. Rich., *H. pulogense* Merr., *H. beccarii* N. Robson.

Basic chromosome number : 12 ; ploidy 2×.

Sect. 27. ***ADENOSEPALUM*** Spach

HYPERICUM sect. ADENOSEPALUM Spach in Annls Sci. nat., sér. 2, Bot. 5 : 357 (1836) excl. *H. elegans* Stephan ex Willd., *H. linarifolium* Vahl *'linearifolium'*, *H. hyssopifolium* Vill., *H. serpyllifolium* Lam., *H. pulchrum* L., *H. nummularium* L., *H. formosum* Kunth, *H. triplinerve* Vent. Type : *H. montanum* L. ; lectotype, see N. Robson in Notes R. Bot. Gdn, Edinb. 27 : 195 (1967).

Hypericum sect. *Perforaria* Choisy, Prodr. Monogr. Hypér. : 37, 44 (1821) ; in DC., Prodr. 1 : 546 (1824) pro parte, quoad *H. tomentosum* L., *H. lanuginosum* Lam., *H. glandulosum* Aiton, *H. reflexum* L.f., *H. montanum* L., *H. lusitanicum* Poiret, *H. elodeoides* Choisy, *H. aethiopicum* Thunb., *H. napaulense* Choisy.

Hypericum A. *Hyperineae* b. *Hypericum* γ *Adenosepalum* (Spach) Endl., Gen. Pl. : 1032 (1840), *status ignot.*, excl. spec. supra cit. sub *Hypericum* sect. *Adenosepalum* Spach.

Hypericum sect. *Euhypericum* Godron in Gren. & Godron, Fl. France 1 : 314 (1847), *nom. invalid.*, pro parte, quoad *H. tomentosum* L., *H. montanum* L.

Hypericum sect. *Euhypericum* subsect. *Triadenioides* (Jaub. & Spach) Boiss., Fl. Orient. 1 : 786 (1867) *'Triadenioidea'*, pro parte, quoad *H. athoum* Boiss. & Orph. – Nyman, Consp. Fl. Eur. : 134 (1878) *'Hypericum'* pro nom. sect., pro parte. – R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6) : 212 (1893) ; op. cit., ed. 2, 21 : 178 (1925) pro parte, quoad *H. cuisinii* Barbey, *H. sanctum* Degen.

Hypericum sect. *Euhypericum* subsect. *Taeniocarpium* (Jaub. & Spach) Boiss., tom. cit. : 787 (1867) *'Taeniocarpia'* pro parte, quoad *H. montanum* L., *H. delphicum* Boiss. & Heldr., *H. lanuginosum* Lam., *H. atomarium* Boiss., *H. scabrellum* Boiss., *H. pestalozzae* Boiss., *H. sinaicum* Steudel & Hochst. ex Boiss. – Nyman, tom. cit. : 132 (1878), *'Hypericum'* pro nom. sect., pro parte, quoad *H. montanum* L., *H. delphicum* Boiss. & Heldr. *H. atomarium* Boiss., *H. tomentosum* L., *H. caprifolium* Boiss.

Adenosepalum (Spach) Fourr. in Annls Soc. linn. Lyon, nouv. sér. 16 : 352 (1868), excl. *A. pulchrum* (L.) Fourr., *A. nummularium* (L.) Fourr., *A. hirsutum* (L.) Fourr.

Hypericum sect. *Hypericum* subsect. *Coridium* sensu Nyman, tom. cit. : 134 (1878) *'Coridia'* pro parte, quoad *H. lusitanicum* Poiret, non Boiss.

Ascyrum sensu Engler in Engler & Prantl, Natürl. PflFam. 3 (6) : 208 (1893) ; op. cit., ed. 2, 21 : 174 (1925) pro parte, quoad *A. filicaule* Dyer.

Hypericum sect. *Euhypericum* subsect. *Homotaenium* R. Keller in Engler & Prantl, op. cit. 3 (6) : 212 (1893) ; op. cit., ed. 2, 21 : 178 (1925) pro parte, quoad *H. pestalozzae* Boiss., *H. montanum* L., *H. aethiopicum* Thunb., *H. elodeoides* Choisy, *H. intermedium* Steudel, *H. delphicum* Boiss. & Heldr., *H. lanuginosum* Lam., *H. atomarium* Boiss., *H. scabrellum* Boiss., *H. sinaicum* Steudel & Hochst. ex Boiss., *H. tomentosum* L., *H. pubescens* Boiss., *H. caprifolium* Boiss., *H. naudinianum* Coss., *H. coadunatum* C. Smith ex Link, *H. monanthemum* Hook. f. & Thomson ex Dyer, *H. reflexum* L. f., *H. taubertii* Barbey, *H. lusitanicum* Poiret, *H. atlanticum* Coss.

Hypericum sect. *Acaulopteron* Acloque, Fl. France : 173 (1894) excl. parte, quoad *H. tomentosum* L., *H. montanum* L. Type : *H. montanum* L. ; lectotype.

Hypericum sect. *Reflexa* Stef. in God. Agr.-les. Fak. Univ. Sofiya 11 : 148 (1933). Type : *H. reflexum* L. f. ; lectotype.

Hypericum sect. *Montana* Stef., tom. cit. : 162 (1933) excl. parte (d). Type : *H. montanum* L. ; lectotype.

Hypericum sect. *Perforata* Stef., tom. cit. : 174 (1933) pro parte, quoad *H. tomentosum* L., *H. lusitanicum* Poiret, *H. pubescens* Boiss.

Hypericum sect. *Euhypericum* subsect. *Oligostema* series *Humifusa* Gorschk. in Shishkin & Bobrov, Fl. U.R.S.S., 15 : 219 (1949), *sine descr. lat.*, pro parte, quoad *H. formosissimum* Takht.

Hypericum sect. *Euhypericum* subsect. *Homotaenium* series *Montana* Gorschk., tom. cit. : 245 (1949), *sine descr. lat.*, excl. *H. venustum* Fenzl.

Hypericum sect. *Homotaenium* series *Adenosepala* Y. Kimura in Nakai & Honda, Nova, Fl. Jap. 10 : 136 (1951) excl. parte, quoad typum. Type : *H. montanum* L. ; holotype.

Hypericum sect. *Humifusoideum* sensu N. Robson in Kew Bull. 12 : 436 (1958) pro parte, quoad *H. kiboense* Oliv., *H. conjunctum* N. Robson non *H. conjunctum* Y. Kimura, *H. aethiopicum* Thunb., non R. Keller.

Type : *H. montanum* L.

Distribution : Canary Is., Madeira, Africa, Europe, S.W. Asia, India to China and Thailand.

About 33 *species* : including *H. glandulosum* Aiton, *H. reflexum* L. f., *H. kiboense* Oliver, *H. conjungens* N. Robson, *H. aethiopicum* Thunb., *H. annulatum* Moris, *H. montanum* L., *H. decaisneanum* Coss. & Daveau, *H. delphicum* Boiss. & Heldr., *H. athoum* Boiss. & Orph., *H. atomarium* Boiss., *H. cuisinii* Barbey, *H. lanuginosum* Lam., *H. huber-morathii* N. Robson, *H. minutum* P. H. Davis & Poulter, *H. formosissimum* Takht., *H. somaliense* N. Robson, *H. tomentosum* L., *H. pubescens* Boiss., *H. sinaicum* Steudel & Hochst. ex Boiss., *H. coadunatum* C. Smith ex Link, *H. caprifolium* Boiss., *H. elodeoides* Choisy, *H. wightianum* Wall. ex Wight & Arn., *H. napaulense* Choisy, *H. filicaule* (Dyer) N. Robson ; also *H. psilophytum* (Diels) Maire ?

Basic chromosome numbers : 9, 8 ; ploidy 2×.

Sect. 28. ***ELODES*** (Adans.) W. Koch

HYPERICUM sect. ELODES (Adans.) W. Koch, Syn. Fl. Germ. Helv., ed. 2, 1 : 148 (1843).

Elodes Adans., Fam. Pl. 2 : 444, 553 (1763), excl. '*Hypericum* 9. Lin. Sp. 784'. – Juss., Gen. Pl. : 255 (1789) '*Elodea*'. – Spach in Annls Sci. nat., sér. 2, Bot. 5 : 171, 353 (1836) ; Hist. Nat. Vég., Phan. 5 : 369 (1836). – Reichenb., Deutsche Botaniker 1 : 211 (1841) '*Helodea*'. Type : *E. palustris* Spach (≡*Hypericum elodes* L.) ; lectotype, see Spach in Annls Sci. nat., sér. 2, Bot. 5 : 172 (1836).

Martia Sprengel, Anl. Kennt. Gewächse, ed. 2, 2 : 788 (1818), *nom. superfl.*, quoad '*Elodea* Adans.' pro parte. Type : *Hypericum elodes* L. ; lectotype.

Hypericum sect. *Perforaria* Choisy, Prodr. Monogr. Hypér. : 37, 44 (1821) ; in DC., Prodr. 1 : 546 (1824) pro parte, quoad *H. elodes* L.

Elodes b. *Elodes* (Adans.) Endl., Gen. Pl. : 1034 (1840), *stat. ignot.*, '*Elodea*' pro nom. gen.

Tripentas Casp. in Mber. K. preuss. Akad. Wiss. 1857 : 43 (1857) ; in Jb. wiss. Bot. 1 : 497 (1858), *nom. superfl.* Type : *Elodes palustris* Spach (≡*Hypericum elodes* L.) ; holotype.

Spachelodes Y. Kimura in J. Jap. Bot. 11 : 832 (1935) *nom. superfl.* Type : *S. elodes* (L.) Y. Kimura (≡*Hypericum elodes* L.) ; holotype.

Type: *H. elodes* L.

Distribution: Azores, W. Europe.

1 *species*: *H. elodes* L.

Basic chromosome number: 8; ploidy 4×.

Sect. 29. ***BRATHYS*** (Mutis ex L. f.) Choisy

HYPERICUM sect. BRATHYS (Mutis ex L. f.) Choisy, Prodr. Monogr. Hypér.: 38, 58 (1821); in DC., Prodr. 1: 553 (1824) excl. *H. revolutum* Vahl, *H. axillare* Lam., *H. nitidum* Lam., *H. fasciculatum* Lam.

Brathys Mutis ex. L. f., Suppl.: 43, 268 (1781). Type: *B. juniperina* L. f. (≡*Hypericum brathys* Smith, *nom. superfl.*); holotype.

Hypericum sect. *Perforaria* Choisy, op. cit.: 37, 44 (1821); in DC., tom. cit.: 546 (1824) pro parte, quoad *H. thymifolium* Kunth, non *H. thymifolium* Banks & Solander, (≡*H. humboldtianum* Steudel).

Hypericum C. *Brathydineae* n. *Brathys* (Mutis ex L. f.) Endl., Gen. Pl.: 1033 (1840), *status ignot.*, pro parte, quoad typum et spec. Jussiaei.

Hypericum sect. *Brathys* subsect. *Eubrathys* R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6): 214 (1893); op. cit., ed. 2, 21: 181 (1925), *nom. invalid.*, excl. *H. nitidum* Lam., *H. gnidioides* Seeman, *H. silenoides* Juss. non sensu R. Keller, *H. epigeium* R. Keller, *H. rigidum* St.-Hil., *H. chamaemyrtus* Triana & Planchon '*chamaemyrtos* Triana', *H. rufescens* Klotzsch, *H. pelleterianum* St.-Hil., *H. myrianthum* Cham. & Schlecht. Type: *H. brathys* Smith, *nom. superfl.*; lectotype.

Sarothra sect. *Brathys* (Mutis ex L. f.) Y. Kimura in Nakai & Honda, Nova Fl. Jap. 10: 232 (1951).

Type: *H. brathys* Smith, nom. superfl.* (=*H. juniperinum* Kunth ?).

Distribution: Central and South America (northern Andes, Roraima), Cuba, Hispaniola.

About 48 *species*: including *H. styphelioides* A. Rich., *H. jahnii* R. Keller, *H. lancifolium* Gleason, *H. roraimense* Gleason, *H. magniflorum* Cuatrec., *H. stenoclados* Cuatrec., *H. carinosum* R. Keller, *H. phellos* Gleason, *H. stenopetalum* Turczj., *H. platyphyllum* Gleason, *H. mexicanum* L. f., *H. pimelioides* Planchon & Linden ex Triana & Planchon, *H. juniperinum* Kunth, *H. strictum* Kunth, *H. struthiolifolium* Juss., *H. weberbaueri* R. Keller, *H. thuyoides* Kunth, *H. hartwegii* Benth., *H. myricariifolium* Hieron., *H. laricifolium* Juss., *H. bryoides* Gleason, *H. andinum* Gleason, *H. quitense* R. Keller, *H. loxense* Benth., *H. lycopodioides* Triana & Planchon, *H. sabiniforme* Trev., *H. goyanesii* Cuatrec., *H. tamanum* Cuatrec., *H. baccharoides* Cuatrec., *H. cuatrecasii* Gleason, *H. ericifolium* Steyerm., *H. garciae* Pierce, *H. lancioides* Cuatrec., *H. meridense* Steyerm., *H. millefolium* Urban & Ekman, *H. prostratum* Cuatrec., *H. pseudocaracasanum* Steyerm., *H. pycnophyllum* Urban, *H. stuebelii* Hieron., *H. tetrastichum* Cuatrec., *H. humboldtianum* Steudel, *H. aciculare* Kunth, *H. caracasanum* Willd.

Basic chromosome number: 12; ploidy 2×, 3× ?

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* *H. juniperinum* Kunth has a different type from *Brathys juniperina* L. f. (≡*H. brathys* Smith) but may be a taxonomic synonym of it.

Sect. 30. ***SPACHIUM*** (R. Keller) N.Robson

HYPERICUM sect. SPACHIUM (R. Keller) N. Robson, *stat. nov.*

Sarothra L., Spl. Pl. : 272 (1753) ; Gen. Pl., ed. 5 : 133 (1754). Type : *S. gentianoides* L. (≡*Hypericum gentianoides* (L.) Britton, Sterns & Poggenb.) ; holotype.

Ascyrum L., op. cit. : 787 (1753) ; op. cit. : 342 (1754) pro parte, quoad *A. villosum* L. et *A. crux-andreae* L. pro parte, quoad syn.

Knifa Adans., Fam. Pl. 2 : 444, 541 (1763). – Vent., Tabl. Regne Vég. 3 : 144 (1799) '*Kniffa*'. Type : *Hypericum mutilum* L., ; lectotype, see Y. Kimura in Nakai & Honda, Nova Fl. Jap. 10 : 233 (1951) (as *Sarothra mutila* (L.) Y. Kimura).

Hypericum sect. *Perforaria* Choisy, Prodr. Monogr. Hypér. : 37, 44 (1821) ; in DC., Prodr. 1 : 546 (1824) pro parte, quoad *H. angulosum* Michaux, *H. virgatum* Lam., *H. gramineum* Forster f., *H. connatum* Lam., *H. japonicum* Thunb. ex Murray, *H. dichotomum* Lam., *H. pilosum* Walter, *H. simplex* Michaux, *H. pusillum* Choisy, *H. involutum* (Labill.) Choisy, *H. silenoides* Juss., *H. quinquenervium* Walter, *H. brevistylum* Choisy, *H. canadense* L., *H. brasiliense* Choisy, *H. fastigiatum* Kunth, *H. indecorum* Kunth, *H. tarquense* Kunth.

Martia sensu Sprengel in L., Syst. Veg., ed. 16, 3 : 333 (1826) pro parte, quoad *M. dichotoma* (Lam.) Sprengel, non Sprengel (1818).

Receveura Vellozo, Fl. Flum. : 237 (1829) ; op. cit., Atlas, 5 : t. 119, 120 (1831). Type : R. *cordata* Vellozo (=*Hypericum connatum* Lam.) ; lectotype.

Tridia Korth. in Tijdschr. Natürl. Gesch. Physiol. 3 : 17 (1836). Type : *T. frankenioides* Korthals (=*Hypericum japonicum* Thunb. ex. Murray) ; holotype.

Hypericum C. *Brathydineae* n. *Brathys* (Mutis ex L. f.) Endl., Gen. Pl. : 1033 (1840), *status ignot.*, pro parte, excl. typum et spec. Jussiaei.

Hypericum sect. *Brathys* subsect. *Connatum* R. Keller in Engler & Prantl, Natürl. PflFam. 3 (6) : 214 (1893). Type : *H. connatum* Lam. ; holotype.

Hypericum sect. *Brathys* subsect. *Multistamineum* R. Keller, op. cit. 3 (6) : 214 (1893). Type : *H. pilosum* Walter '*pilosum* Michx.' (=*H. setosum* L.) ; lectotype.

Hypericum sect. *Brathys* subsect. *Spachium* R. Keller, op. cit. 3 (6) : 214 (1893) ; op. cit., ed. 2, 21 : 181 (1925) excl. *H. hellwigii* Lauterb., *H. wilmsii* R. Keller, *H. collinum* Schlecht. & Cham., *H. adpressum* W. Barton ('Bast.') – Rodríguez-Jiménez in Mems Soc. Cienc. nat. La Salle, 33 (94–95) : 47 (1973). Type : *H. sarothra* Michaux (≡*H. gentianoides* (L.) Britton, Sterns & Poggenb.) ; lectotype, see Y. Kimura in Nakai & Honda, Nova Fl. Jap. 10 : 233 (1951).

Sanidophyllum Small in Bull. Torrey Bot. Cl. 51 : 391 (1924) – P. Adams in Rhodora 64 : 232 (1962). Type : *S. cumulicola* Small (≡*Hypericum cumulicola* (Small) P. Adams) ; holotype.

Sarothra sect. *Trigynobrathys* Y. Kimura, tom. cit. : 233 (1951). Type : *S. myriantha* (Cham. & Schlecht.) Y. Kimura (≡*Hypericum myrianthum* Cham. & Schlecht.) ; holotype.

Sarothra sect. *Spachium* (R. Keller) Y. Kimura, tom. cit. : 233 (1951).

Sarothra sect. *Spachium* series *Eusarothra* Y. Kimura, tom. cit. : 233 (1951) *nom. invalid.* Type : *S. gentianoides* L. (≡*Hypericum gentianoides* (L.) Britton, Sterns & Poggenb.) ; holotype.

Sarothra sect. *Spachium* series *Knifa* (Adans.) Y. Kimura, tom. cit. : 233 (1951) '*Kniffa*'.

Sarothra sect. *Spachium* series *Japonica* Y. Kimura, tom. cit. : 233 (1951). Type : *S. japonica* (Thunb. ex Murray) Y. Kimura (≡*Hypericum japonicum* Thunb. ex Murray) ; holotype.

Type : *H. gentianoides* (L.) Britton, Sterns & Poggenb.

Distribution : America, tropical and south Africa, Madagascar, tropical and east Asia, Australia, New Zealand, New Caledonia, Hawaii ; west and central Europe (adventive ?).

About 54 *species*: including *H. meridionale* L. B. Smith, *H. teretiusculum* St.-Hil., *H. gymnanthum* Engelm. & Gray, *H. mutilum* L., *H. boreale* (Britton) E. P. Bicknell, *H. japonicum* Thunb. ex Murray, *H. connatum* Lam., *H. caprifoliatum* Cham. & Schlecht., *H. cordiforme* St.-Hil., *H. ternum* St.-Hil., *H. rigidum* St.-Hil., *H. denudatum* St.-Hil., *H. cavernicola* L. B. Smith, *H. gnidioides* Seeman, *H. pinetorum* Standley, *H. galinum* Blake, *H. drummondii* (Grev. & Hook.) Torrey & Gray, *H. gentianoides* (L.) Britton, Sterns & Poggenb., *H. pauciflorum* Kunth, *H. diffusum* Rose, *H. lalandii* Choisy, *H. sellowianum* R. Keller, *H. microlicioides* L. B. Smith, *H. legrandii* Arechav., *H. chamaemyrtus* Triana & Planchon, *H. denticulatum* Walter, *H. setosum* L., *H. cumulicola* (Small) P. Adams, *H. rivulare* Arechav., *H. globuliferum* R. Keller, *H. humbertii* Staner, *H. scioanum* Chiov., *H. oligandrum* Milne-Redh., *H. perrieri* N. Robson, *H. fuertesii* Urban, *H. diosmoides* Griseb., *H. dichotomum* Lam., *H. arenarioides* A. Rich., *H. brasiliense* Choisy, *H. pleiostylum* Rodr.-Jim., *H. hilaireanum* L. B. Smith, *H. piriai* Arechav., *H. myrianthum* Cham. & Schlecht., *H. notiale* L. B. Smith, *H. pelleterianum* St.-Hil., *H. brevistylum* Choisy, *H. majus* (A. Gray) Britton, *H. canadense* L., *H. anagalloides* Cham. & Schlecht., *H. polyanthemum* Klotzsch ex Reichardt, *H. silenoides* Juss., *H. philonotis* Cham. & Schlecht., *H. gramineum* Forster f.

Basic chromosome numbers: 12, 9, 8, 7; ploidy 2×, 3× ?

OTHER NAMES FOR INFRAGENERIC TAXA IN *HYPERICUM*

The following names applying to infrageneric taxa in *Hypericum*, as herein understood, have also been published. Either they include more than one of the sections listed above or their type is uncertain.

1. *Hypericaceae* trib. *Desmostemoneae* 'sect'. *Elodeineae* Spach in Annls Sci. nat., sér. 2, Bot. 5: 353 (1836) *nom. invalid.* pro parte, excl. '*Elodea* Spach'.

   Hypericineae (2) *Hypericeae* (c) *Vismieae* (α) *Elodeinae* Reichenb., Handbuch. Nat. Pflanzensyst.: 308 (1837) pro parte, excl. '*Elodea* Adans.'

   Elodes sensu Endl., Gen. Pl.: 1033 (1840) pro parte, excl. 'a. *Elodea* Spach', '*Elodea*'.

   Hypericaceae subfam. *Vismioideae* trib. *Elodeae* Y. Kimura in Nakai & Honda, Nova Fl. Jap. 10: 18 (1951) pro parte, excl. *Triadenum* Raf.

   (All include *Elodes* Adans., *Triadenia* Spach.)

2. *Hypericaceae* trib. *Hypericeae* 'sect.' *Drosanthineae* Spach, tom. cit.: 354 (1836), *nom. invalid.*

   Hypericineae (2) *Hypericeae* (b) *Hypericeae genuinae* (α) *Drosantheae* Reichenb., tom. cit.: 307 (1837).

   Hypericum a. *Drosanthinae* (Spach) Endl., tom. cit.: 1032 (1840), *status ignot.*

   (Comprises *Eremosporus* Spach ('*Eremocarpus*' Reichenb., sphalm.), *Drosanthe* Spach.)

3. *Hypericaceae* trib. *Hypericeae* 'sect'. *Hypericineae* Spach, tom. cit. : 355 (1836), *nom. invalid.*
   Hypericineae (2) *Hypericeae* (b) *Hypericeae genuinae* (β) *Androsaemeae* Reichenb., tom. cit. : 307 (1837) pro parte.
   Hypericum A. *Hyperineae* (Spach) Endl., tom. cit. : 1032 (1840), *status ignot.*
   Hypericaceae subfam. *Hypericoideae* trib. *Hypericeae* Y. Kimura in Nakai & Honda, Nova Fl. Jap. 10 : 21 (1951) excl. parte.
   (Comprises *Webbia* Spach, *Hypericum* sensu Spach and Y. Kimura, *Olympia* Spach.)

4. *Hypericaceae* trib. *Hypericeae* 'sect'. *Androsaemineae* Spach, tom. cit. : 359 (1836) ; *nom. invalid.*
   Hypericineae (2) *Hypericeae* (b) *Hypericeae genuinae* (β) *Androsaemeae* Reichenb., tom. cit. : 307 (1837) excl. parte.
   Hypericum B. *Androsaeminae* (Spach) Endl., tom. cit. : 1033 (1840), *status ignot.*
   Hypericaceae subfam. *Hypericoideae* trib. *Androsaemeae* Y. Kimura in Nakai & Honda, Nova Fl. Jap. 10 : 20 (1951) 'Anrosaemeae'.
   Hypericaceae subfam. *Hypericoideae* trib. *Hypericeae* Y. Kimura, tom. cit. : 21 (1951) pro parte.
   (Comprises *Campylopus* Spach, *Psorophytum* Spach, *Androsaemum* Duhamel, *Eremanthe* Spach, *Campylosporus* Spach, *Norysca* Spach, *Roscyna* Spach, *Takasagoya* Y. Kimura.)

5. *Hypericaceae* trib. *Hypericeae* 'sect.' *Brathydineae* Spach, tom. cit. : 364 (1836), *nom. invalid.*
   Hypericineae (2) *Hypericeae* (b) *Hypericeae genuinae* (γ) *Brathydeae* Reichenb., tom. cit. : 308 (1837).
   Hypericum C. *Brathydineae* (Spach) Endl., tom. cit. : 1033 (1840).
   Hypericaceae subfam. *Hypericoideae* trib. *Sarothreae* Y. Kimura in Nakai & Honda, Nova Fl. Jap. 10 : 23 (1951).
   Hypericaceae subfam. *Hypericoideae* trib. *Ascyreae* Y. Kimura, tom. cit. : 24 (1951) pro parte.
   (Comprises *Myriandra* Spach, *Brathydium* Spach, *Brathys* Mutis ex L. f., *Sarothra* L., *Isophyllum* Spach.)

6. *Hypericaceae* trib. *Hypericeae* 'sect.' *Ascyrineae* Spach, tom. cit. : 368 (1836), *nom. invalid.*
   Hypericineae (2) *Hypericeae* (a) *Ascyreae* Reichenb., tom. cit. : 307 (1837).
   Hypericaceae subfam. *Hypericoideae* trib. *Ascyreae* Y. Kimura in Nakai & Honda, Nova Fl. Jap. 10 (1951) excl. parte.
   (Comprises *Ascyrum* L.)

7. *Petalanisia* Raf., Fl. Tellur. 3 : 80 (1837).
   Pleurenodon Raf., loc. cit. (1837).
   (Types of both genera unknown.)

TAXA EXCLUDED FROM *HYPERICUM*

Triadenum Raf. (in Medic. Reposit., N.Y., 2nd Hexadr., 5 : 352 (1808) *nom. nud.*), Fl. Tellur. 3 : 78 (1837), non *Triadenia* Spach (1836).

Gardenia Colden apud Garden in Ess. Obs. Phys. Lit. Edinb. 2 : 2 (1756) non *Gardenia* J. Ellis (1761), *nom. cons.*

Elodea sensu Pursh, Fl. Amer. Septentr. : 379 (1814), non *Elodea* Michaux, Fl. Bor.-Am. 1 : 20 (1803), nec sensu Juss., Gen. Pl. : 255 (1789) et Vent., Tabl. Regne Vég. 3 : 144 (1799), nec sensu Jack, Malayan Misc. 2 (7) : 25 (1822) et in Hooker's J. Bot. 1 : 371 (1834) pro parte, excl. typ. ; nec. *Elodes* Adanson, Fam. Pl. 2 : 444, 553 (1763). – Nutt., Gen. N. Amer. Pl. 2 : 17 (1818). – Spach in Annls Sci. nat. sér. 2, Bot. 5 : 165, 353 (1836) ; Hist. Nat. Vég., Phan. 5 : 363 (1836).

Martia Sprengel, Anl. Kennt. Gewächse, ed. 2, 2 : 788 (1818), *nom. illegit.*, pro parte, quoad *H. virginicum* L. ; in L., Syst. Veg., ed. 16, 3 : 333 (1826) pro parte, quoad *M. petiolata* (Walter) Sprengel, *M. campanulata* (Walter) Sprengel.

Hypericum sect. *Elodea* Choisy, Prodr. Monogr. Hypér. : 37, 43 (1821) excl. *H. articulatum* Lam.; in DC., Prodr. 1 : 546 (1824). – R. Keller in Engler & Prantl., Natürl. PflFam., 3 (6) : 209 (1893) ; op. cit., ed. 2, 21 : 175 (1925).

Thornea Breedlove & McClintock in Madroño 23 : 369 (1976).

Cratoxylum sect. ***Tridesmos*** (Choisy) Dyer in Hook. f., Fl. Brit. Ind. 1 : 258 (1874).

Hypericum sect. *Ascyreia* Choisy, Prodr. Monogr. Hypér. : 37, 38 (1821) pro parte, quoad *H. biflorum* Lam.

Elodea sensu Jack, Malayan Misc. 2 (7) : 25 (1822) ; in Hooker's J. Bot. 1 : 371 (1834) pro parte, excl. *E. aegyptica* (L.) Jack (*'Egyptiaca'*).

Hypericum sect. *Tridesmos* Choisy in DC., Prodr. 1 : 546 (1824) excl. *H. articulatum* Lam.

Tridesmis Spach in Annls Sci. nat., sér. 2, Bot. 5 : 351 (1836) ; Hist. Nat. Vég., Phan. 5 : 358 (1836) non *Tridesmis* Lour. (1790).

Cratoxylum sect. *Tridesmis* Engler in Engler & Prantl, Natürl. PflFam. 3 (6) : 216 (1893) ; op. cit., ed. 2, 21 : 184 (1925) *'Cratoxylon'*.

Eliea Cambess. in Ann. Sci. nat. 20 : 400, t. 13 (1830).

Hypericum sect. *Elodea* Choisy, Prodr. Monogr. Hypér. : 37, 43 (1821) pro parte, quoad *H. articulatum* Lam.

Hypericum sect. *Tridesmos* Choisy in DC., Prodr. 1 : 546 (1824) pro parte, quoad *H. articulatum* Lam.

PROVISIONAL KEY TO SECTIONS OF *HYPERICUM*

The following key to the sections of *Hypericum* enumerated above must, for reasons already given, be regarded as provisional. It is intended to be complementary to the evolutionary diagrams (Figs 3, 4) and the sectional synonymy and should enable most species to be allocated to a section. However, although the various parts of 'sect. *Euhypericum*' (i.e. Sects 8–19, 26–27) can be grouped fairly easily in their respective evolutionary lineages, it has not always proved easy to define these lineages or key them out. The parts of the key concerned with these groups should therefore be used with particular care.

- Petals and stamens, or only petals (20. *Myriandra*, part), deciduous after anthesis* :
  - Black or red glands absent ; leaves decussate :
    - Stamens in fascicles ; styles free, spreading or ± united ; perianth 5-merous :
      - Flowers homostyled ; stamen filaments free to near base :
        - Styles 5 (4) ; stem lines decurrent from leaf midrib stronger or present alone :
          - Bracteoles appressed to calyx ; styles 4 (5) ; stems and leaves verrucose 2. *Psorophytum*
          - Bracteoles not appressed to calyx ; styles 5 ; stem and leaves smooth :
            - Styles free or partly united ; anthers clearly dorsifixed . . 3. *Ascyreia*
            - Styles completely united ; anthers apparently basifixed . 4. *Takasagoya*
        - Styles 3 ; stem lines decurrent from between leaves stronger or present alone 5. *Androsaemum*
      - Flowers heterostyled ; stamen filaments united to above middle . 25. *Adenotrias* (part)
    - Stamens in a continuous broad ring ; styles adpressed, apparently united ; perianth 5–4-merous . . . . 20. *Myriandra*
  - Black or red glands present on sepal and sometimes petal margin : leaves in whorls of 3–4 19. *Coridium* (part)
- Petals and stamens persistent after anthesis :
  - Stamens in a continuous narrow ring (or irregularly arranged when few) ; black or red glands absent ; placentation parietal ; stem 4-lined or 4-winged, at least when young :
    - Flowers solitary or rarely 2–4 ; plant often branching pseudo-dichotomously ; leaf margin flat or incurved to involute, or very rarely revolute ; shrubs or wiry shrublets, usually with short internodes . . . . 29. *Brathys*
    - Flowers ± numerous, in dichasial to monochasial cymes, or solitary by reduction ; leaf margin flat or recurved to revolute, or very rarely involute ; suffrutices or perennial to annual herbs, rarely with short internodes . . . . . . 30. *Spachium*
  - Stamens in fascicles or irregularly arranged ; other characters not correlated as above :
    - Styles appressed (at the base at least) or ± united, mostly 5 :
      - Plant a tree or shrub ; black glands often present . . . . 1. *Campylosporus*
      - Plant an erect perennial herb ; black glands absent :
        - Styles 5 (4) ; stamen fascicles 5 (4) ; leaves free . . . . . 7. *Roscyna*
        - Styles 3 ; stamen fascicles 3 ; leaves perfoliate . . . . 8. *Bupleuroides*
    - Styles free, spreading or ascending, not appressed, mostly 3 :
      - Stamen fascicles 5 ; styles 3 ; broad-leaved shrub without black glands 6. *Inodora*
      - Stamen fascicles 3–4 or stamens irregular or, if fascicles 5, then styles 5 and plant herbaceous or a shrub with black glands :
        - Seeds ± flattened or convolute or caruncuIate at one end, with testa linear-punctulate ; shrubs or sclerophyllous shrublets, mostly without black glands :
          - Leaves with dense tertiary reticulate venation ; style bases not contiguous :
            - Plant a shrub c. 1·3–4 mm tall ; leaves ± narrowly lanceolate, ± acute ; older stem-nodes not swollen . . . . 21. *Webbia*
            - Plant a low rounded shrub up to c. 0·5 m tall ; leaves broadly lanceolate to obovate or subcircular, obtuse to rounded ; older stem-nodes ± swollen 22. *Arthrophyllum*
          - Leaves without visible tertiary reticulate venation (with or without pinnate secondary venation) ; style bases contiguous, though not appressed :
            - Leaves rounded, pinnately veined, ± discolorous, usually petiolate ; young stems reddish . . . . 23. *Triadenioides*

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* Cf. also 1. *Campylosporus* (sometimes tardily deciduous in *H. socotranum* Good and *H. quartinianum* A. Rich.).

Leaves acute to obtuse, 1-veined, concolorous, sessile ; young stems yellowish :

Flowers homostyled ; stamen filaments free to near base ; petals without nectariferous appendage ; lodicules absent . . 24. *Heterophylla*

Flowers heterostyled ; stamen filaments united to above middle ; petals with nectariferous appendage ; 3 lodicules present at base of ovary 25. *Adenotrias* (part)

Seeds tapering or rounded at both ends, with testa variously patterned ; shrubs to herbs, almost always with black glands :

Stamens in 3–5 obscure fascicles or irregularly arranged ; styles 3–5 ; flowers usually solitary at ends of branches or in irregular cymes (i.e. mixed cymes and foliate branches) ; sepals nearly always entire with apex obtuse to rounded 26. *Humifusoideum*

Stamens in 3 (rarely 4–5) definite fascicles ; styles 3 (rarely 4–5) ; flowers nearly always in regular cymes (sometimes reduced to one flower) ; sepals entire or not, apex various :

Sepal marginal glands (nearly always present) flat-topped or (when sessile) elongated along sepal margin ; stems, if herbaceous, terete ; petals often without superficial pale glands :

Petals without nectariferous appendage ; stamen filaments free nearly to base ; lodicules absent . . . . 27. *Adenosepalum*

Petals with trifid nectariferous appendage ; stamen filaments united to above middle ; 3 lodicules present at base of ovary . . 28. *Elodes*

Sepal marginal glands absent or round-topped or (when sessile) round or, if flat-topped (17. *Hirtella*, part), then stem 2-lined ; petals almost always with superficial pale glands :

Seeds with testa reticulate to linear-foveolate ; petals entire or with sessile marginal glands, without glandular cilia ; plant glabrous or rarely leaves papillose . . . . 9. *Hypericum*

Seeds with testa smooth or rugulose to papillose or ribbed or, if reticulate to linear-foveolate, then petals with some glandular cilia ; plant often ± pubescent :

Seeds with testa ± papillose ; anther gland amber ; black glands usually confined to margins of sepals and petals (or petals entire), usually absent from leaves or rarely terminal or forming an intramarginal row :

Petals ± unguiculate, rarely red-tinged or red-veined, with pellucid glandular dots or short streaks only ; stems not creeping or rooting 17. *Hirtella*

Petals not unguiculate, usually ± red-tinged or red-veined, with pellucid glandular lines (sometimes also a few dots or streaks) or without pellucid glands ; stems creeping, often rooting :

Leaves paired ; capsule valves longitudinally vittate 18. *Taeniocarpium*

Leaves in whorls of 3–4 ; capsule valves usually with some lateral vesicles . . . . 19. *Coridium* (part)

Seeds with testa reticulate or foveolate to rugulose or ribbed ; anther gland black (except in 16. *Crossophyllum*, part) ; black glands on sepals, petals and leaves, frequently laminar or forming an intramarginal row, very rarely wholly absent (16. *Crossophyllum*, part) :

Sepals entire or rarely eroded-subentire, without marginal or intramarginal black glands (sometimes with superficial ones) :

Stem, leaves and sepals glabrous ; capsule erect . 10. *Olympia*

Stem, leaves and sepals pubescent ; capsule pendulous 11. *Campylopus*

Sepals gland-fringed or eglandular-fringed or, if entire, then with intramarginal black glands :

Capsule valves with vesicles and/or interrupted vittae or almost smooth ; seeds with testa scalariform-ribbed or rugulose or rarely minutely foveolate :

Seeds with testa scalariform-ribbed or rarely minutely foveolate ; stem usually terete ; plant glabrous or rarely with leaves setose beneath . . . . . . 13. *Drosocarpium*

Seeds with testa rugulose or rarely faintly ribbed or minutely foveolate ; stem 2-lined ; plant often ± pubescent 12. *Origanifolium*

Capsule valves longitudinally vittate or rarely with vittae slightly interrupted ; seeds with testa reticulate-foveolate to linear-foveolate :

Leaves all gland-fringed, auriculate ; styles 3 16. *Crossophyllum*

Leaves entire or only uppermost gland-fringed (and then styles 5), not auriculate :

Styles and stamen fascicles 5 ; sepals glandular fimbriate 15. *Thasia*

Styles and stamen fascicles 3 or rarely 5, but then sepals entire or subentire . . . . . . 14. *Oligostema*

SUMMARY

An outline of the previous classifications of *Hypericum* and related genera is given, followed by a discussion of problems raised by discrepancies between the various systems. It is concluded that :

(1) The tribes Vismieae, Cratoxyleae and Hypericeae are better treated as a subfamily (or possibly as subfamilies) of the Guttiferae or Clusiaceae (Hypericoideae) than as a separate family (Hypericaceae).

(2) The floral anomalies of *Hypericum elodes* L. and the *H. aegypticum* L. group of species are modifications related to specialized insect pollination, and these species should be included in *Hypericum*, not placed in separate genera.

(3) *Hypericum* sect. *Elodea* comprises herbaceous species derived from *Cratoxylum* Blume and should therefore be treated as a separate genus, *Triadenum* Raf.

(4) The flower of *Hypericum* basically has 5 antepetalous stamen fascicles, which have undergone various modifications during the evolution of the genus.

(5) The species with a tetramerous perianth (*Ascyrum* L.) are neither distinct from *Hypericum* nor a monophyletic group and should be included in two quite separate sections of *Hypericum*.

(6) The type species of *Elodes* Adanson is *Hypericum elodes* L. (*Elodes palustris* Spach), not *H. aegypticum* L. *Elodea* Juss. (1789) is an orthographic variant of *Elodes*, not a distinct generic name, and hence does not threaten *Elodea* Michaux (1803).

The relationships and some evolutionary trends in *Hypericum* as thus defined are discussed and tentative diagrams illustrating the evolution of the genus are given.

A provisional sectional classification of *Hypericum* with complete synonymy is elaborated, along with type species, distribution, approximate number of species, and chromosome number(s). The 30 sections recognized are keyed out.

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INDEX

In this index the names of taxa of a rank between family and genus are listed under the family name Hypericaceae, in separate alphabetical series for the tribes, the 'sections', a term misapplied by Spach, and those of unspecified rank. Similarly, under the various generic names, the epithets of taxa of lower rank are listed in separate alphabetical series for each rank, with those applying to subdivisions of genera of unspecified rank listed immediately before those of species, from which they can be distinguished by the fact that they start with capital letters.

The names that are treated as synonyms in this work are printed in italics in this index. Various of the specific names in *Hypericum* not so treated here will be regarded as synonyms in later detailed treatments of the individual sections. Page numbers in bold type indicate the entry for the taxon as to its type, or, in the case of species, the place of listing as a member of a particular section.

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SPHAGNALES OF TROPICAL ASIA

A. EDDY

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SPHAGNALES OF TROPICAL ASIA

BY

A. EDDY

Pp. 357–445 ; 25 *Text-figures* ; 17 *Maps* ; *Plates* 37–40

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SPHAGNALES OF TROPICAL ASIA

By A. EDDY

ABSTRACT

A revision of the Sphagnales known to occur in tropical Asia is presented, including a key to the species. The treatment includes descriptions, text figures and distribution maps of the taxa recognized, together with brief discussions on character assessment and phylogeny.

Important changes in status are: *S. pseudocymbifolium* C. Muell. Hal. to a subspecies of *S. palustre* L.; *S. subrecurvum* Warnst. to a subspecies of *S. cupsidatum* Hoffm.; *S. flaccidifolium* Anne Johnson to a variety of *S. cuspidatum* subsp. *subrecurvum* (Warnst.) A. Eddy; *S. pappeanum* C. Muell. Hal. to a subspecies of *S. strictum* Sullivant.

Nomenclatural changes include: *S. erythrocalyx* sensu A. LeRoy Andr. non Hampe to *S. perichaetiale* Hampe; *S. thailandense* Hansen to *S. robinsonii* Warnst. *S. khasianum* Mitt. is reduced to a synonym of *S. subsecundum* Nees; *S. beccarii* Hampe to *S. perichaetiale* Hampe; *S. squarrosiforme* H. N. Dixon to *S. junghuhnianum* Dozy & Molk.

INTRODUCTION

IN THE course of identifying specimens of Sphagnales from New Guinea and Malaysia it was soon apparent that an area could be delimited which contained a characteristic assemblage of species. Broadly defined, that area corresponds, in popular terminology, to South East Asia, but excludes the temperate part of northern India and Burma whose bryoflora is composed of mainly boreal elements (the 'extratropische Himalaya' *sensu* Warnstorf, 1911). In phytogeographical terms the area, hereafter referred to as tropical Asia, is extended to include New Guinea, and a proportion of the Pacific Islands known to possess moss floras of largely Malaysian affinities (see Map 1). Thus, with certain modifications, latitudes 23½°N and 23½°S, and longitudes 70°E and 160°E (excluding northern Australia) enclose tropical Asia for the purpose of this revision. Of the 17 taxa included, 12 species are confined to tropical Asia (including 5 spp. endemic to Malaysia, 2 endemic to New Guinea). The elements with wider occurrence necessitated a survey of species on a much wider scale and conclusions regarding distribution are based on a world-wide survey.

Although the number of species is not large, one is nevertheless frequently faced with a choice of epithets in current use seemingly applicable to a single taxon. For example, Zanten (1964) applied the specific name *Sphagnum pauciporosum* (disregarding the earlier *S. beccarii*) to the same plant which Hansen (1961, following LeRoy Andrews, 1951) named *S. erythrocalyx*. Confusion of nomenclature and the need of a means for the determination of the *Sphagnum* species within the region defined are the principal reasons for the presentation of this revision.

THE SPHAGNALES

Unique among the Bryophyta, *Sphagnum* L., the sole genus of the order Sphagnales, is sufficiently distinct and well known to render only the briefest definition necessary in this work. Full descriptions and excellent illustrations are plentiful in earlier literature. Nor is it desirable to repeat the major part of the history of

Sphagnology in Europe, except where it has a direct bearing on the Asiatic flora. (For reviews see, for example, Paul in Engler & Prantl, 1923; Warnstorf, 1911; Braithwaite, 1880; Isoviita, 1966).

Essentially subaquatic plants, the Sphagnales share the protean qualities of other groups of similar ecology. In Europe one result was the tendency to describe and assign names to a multiplicity of varieties and forms (*vide*, e.g., Sherrin, 1927). Many of these are of doubtful value and serve only to obscure specific limits. It is not surprising, therefore, that in the opinion of many botanists, including bryologists, *Sphagnum* is a difficult group to be left to the specialist. That opinion could only be reinforced on referring to Warnstorf's treatment of the tropical taxa. Fortunately, relatively few collections of Asiatic material were available to Warnstorf prior to the publication of his *Sphagnologia Universalis*. For widespread taxa, especially *Sphagnum perichaetiale* Hampe, the list of synonyms is impressive, but the geographically restricted species have relatively few unnecessary names.

That the *Sphagnum* flora of tropical Asia could in part be linked with that of other tropical regions was first indicated by LeRoy Andrews (1941b). Warnstorf's herbarium having been largely destroyed in Berlin, Andrews' notes are of particular value, although his conclusions were often too sweeping, especially so where he reduces many species from the southern hemisphere to European equivalents. Moreover, at least one important error was introduced by him, partly on the basis of a specimen in Warnstorf's herbarium that he erroneously considered to be authentic material of *S. erythrocalyx* Hampe (see under *S. perichaetiale*).

Before 1911, literature concerning tropical Asiatic *Sphagnum* consisted only of the descriptions of new species. Of the 42 published names for the region, Warnstorf retained 27 in his monograph. Little further change, except for the addition of new species, was to take place until LeRoy Andrews' papers (from 1937 onwards) appeared. In these, Andrews was primarily concerned with the American flora. His statements regarding taxa from other regions (except subgenera *Sphagnum* and *Rigida*) were in the nature of asides, and suggested identities of Asiatic species with others were presumably provisional. As it turned out, most of his proposals pertaining to these species have proved to be well founded, although the same can hardly be said for his treatment of some of the Antipodal and South American groups. The dangers involved in a revision based on too limited a geographical area are just as great as those to which Andrews succumbed. Insignificant structural variations may then be overvalued just as easily as significant ones may be overlooked if too many taxa are subjected to cursory examination. Johnson's (1959) revision of the Malaysian species suffered from its limited scope, with the result that several new names were added to the Asiatic list. The treatments of the Sphagnales by Sharma (1949) and Gangulee (1969) cover only the Indian flora; Hansen (1961) deals with the Thailand species.

SPHAGNUM L.

Generic Subdivision

Within the order Sphagnales one finds a diversity of structure rendering its members (species) susceptible to a degree of categorization. Earlier attempts to group species of *Sphagnum* were relatively simple and not always well founded. In time, a more or less settled system of subdivision of this large and diverse genus emerged, and relatively minor elaborations have taken place during the last century following the work of Schimper (1876) and his contemporaries. The major groupings established by these workers are essentially those accepted at the present time. Contention arises only regarding the status to be accorded them.

Easily recognizable habit and apparent homogeneity of growth-form have resulted in the general treatment of the Sphagnales as monogeneric. If the principles adhered to by some modern authors on other groups were to be similarly applied here, no doubt a plurality of generic names would be proposed. At least one section (section *Sphagnum* = *Cymbifolia* ; *Inophloea*) has long been recognized as very distinct from the remainder. Even Andrews (1911), whose approach was to simplify whenever possible, suggested the probable generic value of this group. Oddly enough, this section has never been separated at the generic level, in spite of the occurrence of unique characters in its members. On the other hand, the two genera, *Isocladus* Lindb. (1862) and *Hemitheca* Lindb. ex Braithw. (1882), that have been separated from *Sphagnum* were both based on secondary modifications of minor value in the generic sense, and are to be included in subgenus *Isocladus* (= *Litophloea*).

Isoviita (1966 : 207) sees no great disadvantage in maintaining the categories at their normally assigned rank of section. Certainly an elaborate hierarchical system, lacking supporting evidence from the fields of genetics, biochemistry and culture experiments, including hybridization programmes, is to be avoided where the phylogenetic significance of the characters used cannot be properly assessed.

My personal view is that, while there can be no advantage in the gratuitous introduction of new generic names, differentiation of certain groups requires greater emphasis. Therefore, a two-tiered system is proposed wherein the sections *Sphagnum*, *Rigida* and *Homophylla* are treated as subgenera, while *Acutifolia*,* *Subsecunda* and *Cuspidata* are retained as sections within the much larger and more diverse subgenus *Isocladus*. (The latter subgenus would also include *Squarrosa*, *Insulosa* and *Polyclada* in the present context, none of which occurs in Tropical Asia. The African section *Mucronata* requires further appraisal.)

The genus *Sphagnum* is clearly divisible into infrageneric groups and the degree of distinction between sections is variable. Subgenera are based on characteristics which, even if their biological significance is obscure, are unique to each ; it is unnecessary to introduce any new names and only changes in status or reintroductions of previously established rank are needed. It is unfortunate that, in order to conform with the Code, the largest subgenus must be designated *Isocladus* and typified by a rather aberrant species (i.e. *S. macrophyllum* Brid.) but I see no other difficulty in its adoption. In Europe, the disparity between, e.g., sections *Acutifolia* and *Cuspidata* might appear to be just as great as between the proposed subgenera. However, none of the features associated with these sections is absolutely constant when examined on a world-wide scale. Species are known which show affinities to more than one section, *Acutifolia* and *Cuspidata* both merge to some degree with *Subsecunda* (note Andrews (1915) reduces *Subsecunda in toto* to *Cuspidata*) so that there has occasionally been doubt as to which section a species should be assigned (e.g. *S. antaranse* Wijk & Zanten, *S. ceylonicum* Mitt. ex Warnst.).

---

* *Acutifolia*, in the present context, probably deserves subgeneric rank. Raising it to such at this stage would create new problems in the assignment of minor sections, e.g. *Polyclada* and *Squarrosa*, whose relationships are not yet clear.

Examination and Assessment of Characters

There is no general principle to be followed when weighting the significance of characters upon which to base taxa. Those employed in the diagnosis of species in one group may constitute trivial modifications in another. In this order of plants, whose members respond so markedly to environmental changes, it is often difficult and sometimes impossible to distinguish between inherent genetic variability and response to habitat. The latter can be assessed to some degree if sufficient material is available, but the specific value of the former, in the absence of data derived from breeding experiments, remains to some degree a matter of opinion. Below species level, the course followed here seems reasonable : where one or more features of the plants are demonstrably paralleled by a geographical or ecological pattern, they are generally treated as constituting a subspecies or a variety respectively. Experience has shown that very closely related taxa, making similar demands upon their environment, rarely occupy an identical ecological niche *over the same geographical range*. When they appear to do so, they can frequently be shown to be simply genetic races worthy of, at most, varietal distinction. (No formal statistical methods of analysis have been applied, however ; only in a few cases would there be a sufficient quantity of material available.)

Basic information is derived principally from examination of the branch and stem leaves and stem cortex. Branch leaves are always taken from a point on a spreading branch about one-third of its length from the base. Leaves from the base or branch-tip, or from pendent branches, may be slightly or strongly modified in form. Where possible, stem leaves are taken from an internode at a point distant from a fascicle. Hyaline cells are extremely translucent, and it is unsafe to draw conclusions regarding perforation without recourse to staining. Various techniques are available, but I find that, for general purposes, a solution of Methylene Blue in a 50 per cent solution of alcohol, to which a few drops of glycerol have been added, serves as an adequate adsorption stain. Chlorocyst contents stain very darkly while the hyaline cells tend to stain a medium blue, the intensity depending upon the strength of the solution and the duration of immersion. A slight flocculation occurring at times does not hinder observation of fibrils and pores to a noticeable extent in fresh preparations.

Sphagnum leaves alter little on drying, and the leucocysts (hyaline cells) in particular shrink only slightly even under high vacuum. Suitably coated (usually gold or gold-palladium) leaves, stem cortex and spores can be examined under the scanning electron microscope. No new features came to light on specimens so examined, but useful confirmation of light-microscope findings, together with sharply defined, deep-focus photographic records, have been obtained (see also Mozingo *et al.* (1969), who, however, fail in part to allow for artifact when drawing conclusions regarding the rupture of pores, shrinkage furrows, etc. and do not make it clear whether they consistently examine the dorsal or ventral leaf surface, e.g. f. 5 & 6).

In general terms, the archetypal *Sphagnum* plant is most closely represented by, on the one hand, a 'primitive' member of the *Subsecunda* (e.g. *S. luzonense*) and on the other by the *Homophylla* (*S. sericeum*). The latter group is monotypic but the former, or its progenitor, seems to have formed the basis from which all of the other extant species have been derived. Evolutionary patterns among visible structures seem to be logical adaptations to terrestrial rather than aquatic habitats. Consequently, most of the characters upon which species are based are concerned with water movement through the plants' mainly external conducting systems. Types of modification and their taxonomic significance are briefly summarized below.

Branch fascicles. The fasciculate branch system is fundamental to the order and is constant in the Asiatic species. Variation in branch morphology has evolved from a state wherein all the branches of a fascicle are identical and follows two basic trends : one trend is towards simple reduction of one or more branches in size and vigour, usually with some loss of pigmentation (e.g. *S. luzonense* ; the boreal taxa *S. pylaisii* Brid. and *S. cyclophyllum* Sull. & Lesq. are extreme examples in which the branches may be entirely absent), and the other is the modification of 1–3 branches which have become strongly deflexed, with weak, usually unpigmented leaves. The latter, *dimorphic*, condition (in contrast to unmodified, *monomorphic*) is a relatively advanced feature, being constant in subgenus *Sphagnum* and most *Acutifolia* but variable in degree in other groups. Although useful in the study of evolutionary trends, variation in branch morphology rarely offers useful 'key' characters within a Section. The pendent branches of a dimorphic system are featured best in those groups which have a multi-layered stem cortex and is an adaptation to aid external water conduction (i.e. the 'hummock formers' of northern bog vegetation). Monomorphic branches persist in 'primitive' taxa such as *S. sericeum* and *S. ovatum*, and in several subaquatic species.

Branch leaves. Branch-leaf outline is useful in the recognition of subgenera *Sphagnum* and *Homophylla* but is rarely of value in the identification of species, being rather uniform throughout the remaining groups. However, anatomical features of branch leaves, including leucocysts, chlorocysts and pores, are the source of most of the important characteristics upon which the higher taxonomic divisions, and to a large extent species, are based. The leaves of pendent or vestigial branches are variously modified so that the characters represented in the normal branch leaves may be obscured or absent. Consequently no recourse has been made to pendent-branch leaves in this work.

Stem leaves. The archetypal *Sphagnum* is *isophyllous* with little other than width of insertion to distinguish stem leaves from branch leaves. Isophylly is well represented in *S. sericeum* and is a condition which has persisted to a greater or lesser degree in subaquatic *Subsecunda*. Among the majority of *Sphagna* stem leaves have lost their primary features to some extent. Modification may simply involve the partial loss of fibrillae (e.g. in *S. cuspidatum* subsp. *subrecurvum*, Fig. 16) or be so extensive that stem leaves bear no resemblance to branch leaves (e.g. *S. cuspidatulum*, Fig. 18). Species vary in the degree of stability of stem-leaf form, and the frequency with which isophyllous or partially isophyllous ('hemi-isophyllous') states occur. Thus the stem leaves provide valuable taxonomic characters in the more highly evolved *Cuspidata* and temperate *Acutifolia* but among other groups, particularly subgenus *Sphagnum*, minor, insignificant variations have been greatly overvalued. Etiolated or juvenile stems are always isophyllous to a degree and should not be used for the identification of species.

Pores, resorption. In this work the term *pore* is reserved exclusively to describe the perforations of leucocyst walls. Chlorocyst walls are pitted in a manner similar to the cell walls of Musci, a condition described as porose by many authors which is in no way homologous to that pertaining to the leucocysts of *Sphagnum.* (Similar pores are, however, met with in the moss families *Calymperaceae* and *Leucobryaceae*, families which have a tissue organization analogous to that of *Sphagnum*). Pores in leaf, stem and branch leucocysts permit ready translocation of water and ions over the metabolizing net of chlorocysts. They are confined, in the leaves, to free leucocyst surfaces but, in the stem cortex, may occur also in adjacent radial and end walls. Perforation occurs early in the ontogeny of the leucocyst through a process of reabsorption ('resorption') of the cell wall. Pores are usually circular in outline or, in extreme examples, part or all of a cell surface may disappear (e.g. commonly in subgenus *Sphagnum*). Such extended pores are frequently referred to as *resorption gaps* or *membrane gaps* (Fig. 21, C). The same process of resorption is probably responsible for the removal of the primordial leaf apex to give the 'truncate-dentate' apex familiar throughout most of the genus and the '*resorption furrow*' (Fig. 2, E, F) of the subgenus *Sphagnum.* The potential extent of resorption has great evolutionary significance, being one of the principal mechanisms by which *Sphagnum* plants are modified.

Perforation may be incomplete so that circular thinnings ('*shadow pores*'), visible only after careful staining, may occupy sites of normal pores. Rings of thickening wall material which do not bound actual perforations may resemble pores in unstained material and are termed *pseudopores.* They may, as in *S. luzonense* (Pl. 38 E), replace normal pores or simply, as in *S. antarense* (Fig. 11, G), act as additional strengthening of the leucocyst wall.

Taxonomically useful data are supplied by the type of pore (ringed or unringed), pore distribution pattern relative to the leaf surfaces, and, to a lesser extent, the pore diameter, rather than the pore frequency. The value of such data depends very much upon the group involved. For example, the uniporose stem cortex of *S. perichaetiale* is diagnostic, but no significant variation in porosity is evident throughout the remainder of the subgenus *Sphagnum.* Leaf-leucocyst pores help in the discrimination between closely related taxa within section *Cuspidata*, but are seldom to be similarly relied upon in section *Acutifolia* or most of section *Subsecunda.* Pores of the branch cortex are consistent throughout a subgenus. The somewhat specialized 'retort cells', absent in subgenus *Sphagnum*, are present throughout subgenus *Isocladus* but the extreme differentiation apparently diagnostic of the boreal *S. tenellum* (Brid.) Brid. has not been noted in any of the tropical Asiatic species.

Pseudolacunae (*pit pores*). The structures named 'pit pores' by Andrews (1951), sometimes termed 'triple pores', have received only passing mention. These were first depicted in section by Jensen (1915), although they were not mentioned in his text. Andrews (1951) pointed out the presence of these 'pit pores' in subgenus *Sphagnum* and referred to the reported occurrence of a similar feature in subgenus *Rigida*, but seemingly did not investigate further. Not until Hansen published his paper on Thailand Sphagna (1961), where their appearance in transverse section is clearly depicted in a photograph, was any further significant reference made to pit pores. Hansen stressed the need for further investigation, but had not himself fully assessed their diagnostic significance (which would have prevented the error of placing *S. thailandense* in subgenus *Sphagnum* instead of section *Subsecunda*).

To avoid ambiguity, the term 'pseudolacuna' is adopted for this structure since what is referred to by Andrews is seen in transverse section as a more or less spherical hollow space contained in the angle formed between three hyaline cells, and overlying the junction of three chlorocysts (Fig. 1, E ; Pl. 37, E, F). Pseudolacunae are constant features in all species of subgenera *Sphagnum* and *Rigida*, where they occur exclusively, in the former, on the dorsal face of the branch leaves (and stem leaves in isophyllous forms), and in the latter on the ventral face of the branch leaves. Elsewhere in the genus they have been noted only in some members of section *Acutifolia*, where their presence probably indicates an evolutionary link with subgenus *Sphagnum.* The position occupied on the leaf surface in subgenus *Sphagnum* is very regular. Relative to the hyaline cells they are always to be found at the junction formed by the basal angle and two lateral angles of the cells involved, never in the apical angle (Figs 1, G ; 3, G ; Pl. 37, F). Pseudolacunae are not normally very conspicuous in surface view, and are then most noticeable in tropical and southern species, especially where the leaf is largely devoid of normal pores. They are seen to open to the exterior via a three-armed or more or less triangular opening. In boreal species such as *S. palustre,* the aperture may be much wider so that, in surface view, especially towards the leaf apex, the three (occasionally only two) pores constituting the pseudolacuna may be indistinguishable from normal pores. It can be pointed out that in pauciporose forms such as *S. perichaetiale* these pseudolacunae would offer the only means of direct communication to the external environment.

Although inconspicuous in surface view, pseudolacunae are so obvious in transverse leaf sections that it is not a little astonishing that they have so rarely been figured, let alone described. One assumes, for example, that Warnstorf must have observed many hundreds of leaf sections of subgenus *Sphagnum* in preparation of his monograph (1911), yet not one of the large number of drawings in his *Sphagnologia Universalis* shows a pseudolacuna. In view of such omissions, perhaps it is less surprising that casual observers faced with only one or two specimens might pass over the feature as an infrequent aberration, or possibly an artifact.

The biological function of pseudolacunae is obscure. Possibly in boreal subaquatic forms they are relict features. The apertures of those of *S. perichaetiale* and *S. strictum* are found frequently to be almost closed after desiccation (Pls 37, F, 38, C). Tropical species are montane rain-forest, rather than bog-dwelling, plants and it may be tentatively suggested that pores which could be occluded in dry conditions, especially in species with wide hyaline cells, may reduce water loss.

Fibrils. With a few notable exceptions the presence of fibrils is a consistent feature of branch-leaf leucocysts throughout the genus. Their function is to impart rigidity to the leucocysts and to the branch leaves as a whole, preventing collapse and thereby forming a framework to support the chlorocyst net. The form of the fibril is that of a disc with wide central perforation (the 'partial septum' of some authors) or sometimes a helical band, being an ideal structure which does not impede water movement.

Complete absence of fibrils in some species of subgenus *Isocladus* (e.g. *S. macrophyllum* Brid.) is probably a derivative state but there is no reason to assume that subgenus *Homophylla* has been derived from a fibrillose ancestral form. Regarding the other efibrillose taxa, *S. efibrillosum* and *S. novo-caledoniae*, it is not possible, on the small amount of material examined, to venture an opinion.

The extent to which stem leaves may lack fibrils is of taxonomic importance in some groups, particularly section *Cuspidata*, but may have little significance in others. For example, stem leaves of subgenus *Sphagnum*, particularly tropical species, are extremely variable but numerous spurious taxa have been named on the basis of stem-leaf fibrillosity.

Pigments. Secondary pigments occur in most *Sphagna* except in shaded habitats, sometimes more or less confined to antheridial branches. Although sometimes defying verbal description, their presence usually imparts a distinctive appearance to the plants in the field, even rendering some species more readily identifiable in the field than in the laboratory. Thus, while brownish pigmentation occurs almost throughout section *Subsecunda*, the quality and intensity of colouration may be highly specific. *S. antarense*, for example, has peculiar pinkish undertones which at once distinguish it in the field from *S. subsecundum*. Crimson pigments are to be found in some *Subsecunda*, many *Acutifolia* (not prominent in *S. junghuhnianum*) and subgen. *Sphagnum*. If chemically identical in these groups, such pigments may provide strong evidence of evolutionary links between them. Secondary pigments in the Sphagnales would repay comprehensive study.

Phylogeny

It has been customary to arrange the subdivisions of a genus into an order reflecting the authors' opinions of their phylogeny. This has not invariably been the case in treatments of *Sphagnum* but has frequently been implicit in previous systems of classification. It is, of course, impossible to represent a polyphyletic group in a single linear series, even where relationships are clear. It must be made clear, therefore, that the arrangement of subgenera and sections in this paper is not representative of the author's concept of interrelationships between them, or of developmental sequences. For example, subgenus *Sphagnum* is placed first, being the *subgenus typicum generis*, but is generally regarded (by myself included) as probably the most 'advanced' group and would normally be placed last.

Evidence derived from different sources regarding the evolution of the Sphagnales is sketchy and often contradictory, and it is by no means established which morphological characteristics should be regarded as 'primitive' or 'advanced'. Nevertheless, relationships between groups of species within sections, and less obviously between sections themselves, suggest themselves to me even on the basis of the relatively small geographical coverage of the present work, together with a somewhat less detailed familiarity with the European taxa. It is appropriate here to mention some of the more obvious of these, while recognizing the potential weaknesses of ideas formulated without recourse to evidence other than the physical appearance of herbarium specimens and the distribution patterns of the taxa.

With the possible exception of *Sphagnum sericeum* (and disregarding obviously relict, aberrant species) the evolution of *Sphagnum*, i.e. that of the morphological attributes associated with its groups, seems to have been exceptionally slow (see p. 368 below). It is reasonable to assume that peculiarities of structure, where they occur in common among some groups (which on other grounds are separable) probably indicate evolutionary links. Generally uncertain, however, is the sense of these links, that is the actual direction of a sequence, whether apparently more complex groups like subgenus *Sphagnum* are the end products of successive elaborations of structure, or the simpler groups the end products of trends in reduction. Section *Subsecunda* is generally regarded as the most primitive, especially the homophyllous forms with serially or randomly porose leaves, with subgenus *Sphagnum* at the other end of the scale.

Some notes on evolutionary trends are included in the discussion on character weighting (pp. 362–366) above. A phylogenetic diagram (Fig. 25) is given to include the species listed. This scheme, it is hoped, may be elaborated without undue alteration to include the taxa from other geographical regions when they have been examined in their turn. In brief, the earliest divergence is supposed to have occurred between the 'normal' *Sphagnum* type, resembling *Subsecunda* with fibrillose hyaline cells and resorbed leaf apices, and the *Homophylla* type with no fibrillae and more or less unmodified leaf apex. Further evolution and spread has subsequently taken place only in the former group, the earliest segregations being towards *Cuspidata*, on the one hand, and *Sphagnum*, through *Acutifolia*, on the other. No time scale is given, but the primary subgeneric divisions are thought to be very early, probably no later than the Jurassic period.

Origin and Distribution

GENERAL CONSIDERATIONS

LeRoy Andrews (1937) held the opinion that, in the absence of positive data, there was little purpose to be served in speculation on the origins of the Sphagnales. Inevitably, however, conjecture regarding the geographical origin and subsequent migration and differentiation of this large and important order has been made from time to time. Evidence is difficult to assess and statistical approaches involving subjective estimates of modern 'species' are based on shaky foundations, especially where such estimates utilize the varied species concepts of several authors. Fossils are rare, and tell us only that *Sphagnum* in its present form existed in Europe during the Miocene (Straus, 1952 ; leaf fragments) and probably much earlier (Reissinger, 1950). Indeed, to explain the world distribution of *Sphagnum* satisfactorily, it must be assumed that the genus had already evolved to a series of forms, the basis of the major sections, as early as the mid- or late Triassic period. The exceptionally narrow ecological amplitude of the Sphagnales imposes severe restrictions upon the performance of the order in colonization. From what is known of its biology, it can be inferred, moreover, that all but the narrowest seas presented impassable barriers. (The post-Pleistocene spread of *Sphagnum* in the boreal temperate zone was a logical consequence of continuity of land under a favourable climatic regime.)

The distributional history of species is variable, but the broad principle of early spread and isolation can be explained in terms of Wegener's theory of drifting continents, suitably modified to conform with recent geological and geophysical evidence. Two premises consequent to this theory must then be accepted, viz. (a) the more or less cosmopolitan distribution of the genus, already somewhat diversified into major subgeneric divisions, before the break-up of the single 'continent' Pangea (about mid-Triassic) ; (b) a subsequent very slow rate of evolution. (The kind of speciation often assumed to occur in rapidly expanding populations may be held responsible for the development of a number of smaller sections in the boreal zone, e.g. *Polyclada, Insulosa, Squarrosa*, perhaps as recently as the Tertiary period.) Thus, each continental land mass, while sharing subgenera, tends to have its endemic assemblage of species. The degree of similarity between these primitive assemblages reflects in some degree the sequence of isolation from its neighbours.

Tropical asiatic distribution

Tropical Asia has had a very complicated geological history which is reflected in its *Sphagnum* flora, the latter being represented by several phytogeographical elements. The derivation of some of these elements is obvious, but of others rather obscure. For convenience, the various elements are considered separately below.

The regions now represented by India, continental Asia (Burma, Thailand, Indo-China), the Malay Archipelago and New Guinea have each at some time had a separate existence from each other during geological history. Inundations and land connections at different periods have complicated the picture considerably, but basic assemblages of species are discernible.

(1) *Widespread*: A large majority of *Sphagnum* species are confined to their respective continental systems or, in the northern hemisphere, to the boreal zone. I know of only two species that extend into the temperate zones of both hemispheres, *S. fimbriatum* Wils., confined to cool oceanic belts, and *S. magellanicum*. The former species, although present in the Himalayan mountains, does not enter the area under consideration but is reported from New Zealand and South Africa. *S. magellanicum* is widespread in the northern hemisphere ; it is relatively abundant in South America, commonly spreading into the tropical zone, has been collected in two or three of the East African Islands, including Madagascar, but is unknown in Malaysia, continental Africa or Australasia. The occurrence of *S. magellanicum* in northern India and

Taiwan should perhaps be regarded as southern extensions of its Eurasian distribution rather than as relict occurrences of a now disjointed, sub-cosmopolitan pattern, notwithstanding its occurrence in other tropical regions. Then it would be more appropriately listed with, for example, *S. subsecundum* and *S. cuspidatum* subspecies *cuspidatum* below as part of the Eurasian element.

(2) *Pan-tropical*: Two species of *Sphagnum* are known which occur throughout the tropical and sub-tropical zones of continual high humidity, *S. perichaetiale* and *S. strictum sens. lat.* Both are regarded as probably primitive species within their respective subgenera, and their occurrence in Tropical Asia as part of, or relicts of, former widespread populations seems to be acceptable. The occurrence of the latter species in tropical America was *sub judice* until the present time, doubt having been raised as to the geographical origins of at least some of the specimens in the herbarium. However, the African and New Guinea plants approximate so closely phenotypically to at least some proven American specimens of *S. strictum* that they may be amalgamated for our present phytogeographical interpretations.

(3) *Eurasian element*: The major proportion of the tropical Asiatic *Sphagnum* flora is composed of species which, if not identical with temperate Eurasian species, at least are more closely related to these than to the assemblages of other geographical regions. The minority of species which cannot be distinguished from their Eurasian counterparts would seem to have migrated southwards and eastwards during periods of land connections between the Malaysian islands and the continental mainland, probably during the Pleistocene period. Subsequent climatic amelioration severed land connections (eustatic rise in sea-level) and at the same time confined temperate species to the higher mountain systems. The Eurasian element in Malaysia, comprised of *S. subsecundum* and *S. cuspidatum* subspecies *cuspidatum*, is to be regarded, therefore, as composed of Pleistocene relict species. On the continental mainland, on the other hand, the occurrences of the same species are simply the southern limits of their existing widespread Eurasian distribution patterns.

(4) *Indo-Malayan element*: The remaining species which have not been included under the headings (1)–(3), and excluding *S. ceylonicum*, are more or less confined to the area defined in this revision, and can be classified, in broad terms, as Indo-Malayan. Some of the species in this group show strong affinities with European species, especially in the Himalayan region. This is particularly noticeable with *S. ovatum* (cf. *S. subsecundum*), *S. luzonense* (cf. *S. auriculatum* W. P. Schimp. agg.), *S. cuspidatulum* (cf. *S. riparium* and *S. lindbergii*) and *S. junghuhnianum* (cf. *S. subnitens*). The occurrence of intermediate forms, which are rather rare, in the 'transition belt' of the Himalayas would seem to indicate the direct derivation of some species in one direction.

A view that some, at least, of the European species have originated in South East Asia is not incompatible with similar theories regarding the ancestry of flowering plants (*vide*, e.g., A. C. Smith, 1970). It is possible to subdivide this assemblage of species into groups of narrower definition.

(a) *Widespread Indo-Malayan*: Species which, although more or less confined to the area under consideration, are widespread and locally abundant throughout the region. Under this sub-heading are to be included S. *junghuhnianum* and S. *cuspidatulum*, species which are frequently found in association with one another, and which locally dominate the terrestrial vegetation in montane forest zones. Perhaps S. *cuspidatum* subsp. *subrecurvum* should be included here. (Depending upon the criteria chosen, one species may equally well be assigned to one or another group (e.g. S. *magellanicum* above). Within tropical Asia S. *perichaetiale*, a pan-tropical species included under (2) above, would be grouped with (4a), being widespread in the region, but rarely in the quantity of S. *junghuhnianum*.)

(b) *Sub-continental*: A number of exclusively tropical species seem to be largely confined to the continental mainland, extending from North East India and Thailand to Indo-China, sometimes reaching the Philippine Islands, but absent (i.e. unrecorded) from Malaysia. S. *robinsonii* and S. *luzonense* are to be included here, and are the two species of the sub-continental pattern which also occur in the Philippines. The apparent disjunction between Thailand and the Philippines is probably accentuated by the lack of records from Indo-China. It is not impossible that these species occur in Taiwan as migration southwards via Taiwan to the Philippines from the continent during the Pleistocene period was feasible. The other taxa to be listed under this sub-heading are S. *ovatum* and S. *palustre* subsp. *pseudocymbifolium*, both confined to the tropical zone on the continental mainland, and related to the Eurasian complex.

(c) *Malaysian endemics*: The remaining *Sphagna* are endemic species with more or less restricted ranges, in many cases known only from one or two localities. Most of them are palaeoendemic, a proportion of these being somewhat bizarre forms (S. *novo-caledoniae*, S. *efibrillosum*) whose relationships with other living forms are impossible to determine at this stage. S. *sericeum* is probably the most important endemic species since, in view of its apparent antiquity and local frequency, its geographical restriction is puzzling. S. *antarense*, of particular interest phylogenetically, is also to be included here.

S. *novo-guineense* appears to be a classical case of neoendemism, restricted in range because of its recent derivation (from S. *cuspidatulum* ?), rather than by partial extinction. This species does not show the wide divergence from related taxa usually manifest in palaeoendemic *Sphagna*.

(5) *African element*: S. *ceylonicum* is, under that name, a species regarded as endemic to Ceylon, being quite unrelated to any other Asiatic species. However, a complex of forms occurring in East Africa and especially the East African islands contains specimens which very closely resemble the Ceylon plant and are probably conspecific with it. Proposed synonymy has been deferred for reasons already stated, but for the purposes of distributional interpretation, S. *ceylonicum* is to be considered as African (*sens. lat.*, i.e. including Madagascar) in origin. The geological history of India and South East Africa adequately explains the fragmentation of shared populations (Dietz & Holden, 1970). The pronounced dry season of the Indian sub-continent would prevent their spreading northwards.

CONSPECTUS OF TAXA INCLUDED IN THIS WORK

Genus *Sphagnum* L.
  Subgenus *Sphagnum*
    1b. *S. palustre* L. subsp. *pseudocymbifolium* (C. Muell. Hal.) A. Eddy
    2. *S. perichaetiale* Hampe
    3. *S. magellanicum* Brid.

  Subgenus *Isocladus* Lindb.
   Section *Subsecunda* (Lindb.) Schlieph.
    4. *S. subsecundum* Nees
    5. *S. ovatum* Hampe
    6. *S. luzonense* Warnst.
    7. *S. robinsonii* Warnst.
    8. *S. antarense* Zanten
    9. *S. ceylonicum* Warnst.
    10. *S. novo-caledoniae* Paris & Warnst.
    11. *S. efibrillosum* A. LeRoy Andr.

   Section *Cuspidata*
    12a. *S. cuspidatum* Ehrh. ex Hoffm. subsp. *cuspidatum*
    12b(i). *S. cuspidatum* subsp. *subrecurvum* var. *subrecurvum* (Warnst.) A. Eddy
    12b(ii). *S. cuspidatum* subsp. *subrecurvum* var. *flaccidifolium* (Anne Johnson) A. Eddy
    13. *S. cuspidatulum* C. Muell. Hal.
    14. *S. novo-guineense* Fleisch. & Warnst.

   Section *Acutifolia* Wilson
    15. *S. junghuhnianum* Dozy. & Molk.

  Subgenus *Rigida* (Lindb.) Lindb.
    16b. *S. strictum* Sull. subsp. *pappeanum* (C. Muell. Hal.) A. Eddy

  Subgenus *Homophylla* Lindb.
    17. *S. sericeum* C. Muell. Hal.

DESCRIPTION OF TAXA

SPHAGNUM L.

SPHAGNUM L., Sp. Pl. 2 : 1106 (1753) ; Gen. Pl., ed. 5 : 487 (1754) – Hedw., Fund Hist. Nat. Musc. Frond. 2 : 85 (1782).

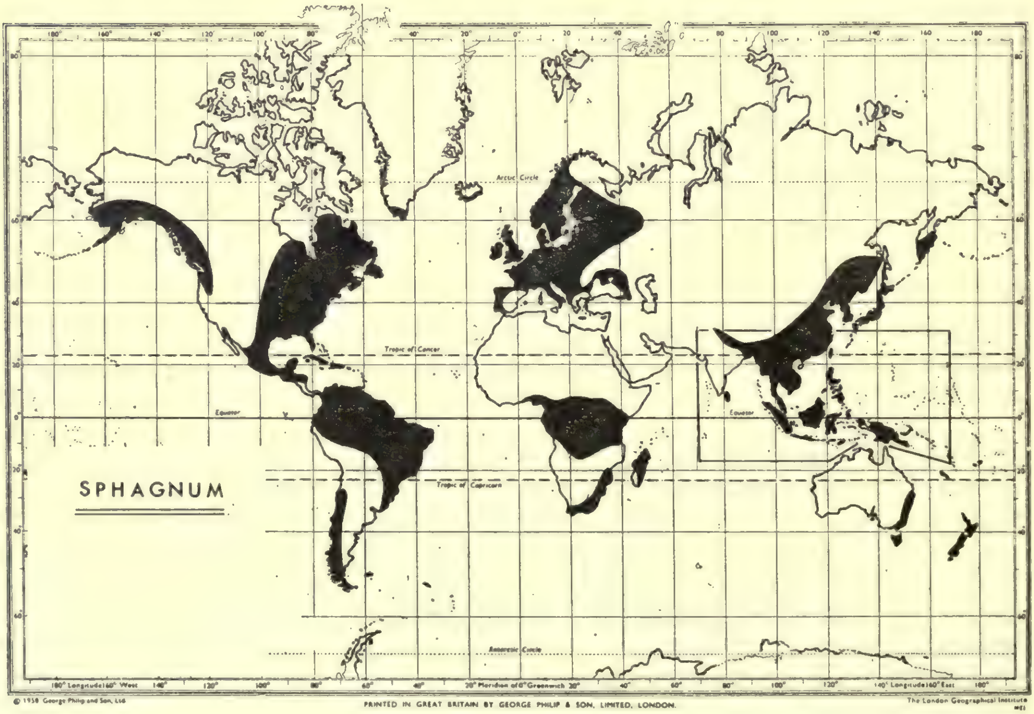
Isocladus Lindb. in Öfvers. K. VetenskAkad. Förh. Stockh. 19 : 133 (1862).
Hemitheca (Braithw.) Lindb., Eur. & N. Amer. Hvitmossor (Sphagna) : 6 (1862).

Lectotype : *S. palustre* L., cf. N. L. Britton, Fl. Bermuda : 431 (1918).

Stems rather weak, not normally self-supporting, with a well-defined cortex of enlarged hyaline cells (leucocysts) in one or more layers ; cortical leucocysts often with pores, occasionally with spiral fibrils (subgen. *Sphagnum*) ; central 'pith' surrounded by a woody cylinder which is non-conducting. Branches arising in fascicles which are aligned into five series with distinct but often short internodes between them (fascicles rarely reduced to a single branch, or absent). Branch leaves unistratose, bordered by one or more series of narrow cells ; areolation of two kinds of cell, i.e. large, inflated hyaline cells (leucocysts) set in a meshwork of narrow, green cells (chlorocysts) the former normally appearing banded by annular or spiral partial septa (fibrils) and variously perforated by pores (fibrils rarely absent, leucocysts rarely entirely devoid of pores).

Monoecious or dioecious, but branches always unisexual. Antheridia pedicellate, in the axils of several leaves on a virtually unmodified branch ; male bracts resembling normal branch leaves or slightly smaller and more intensely pigmented ; paraphyses branched, delicate. Female inflorescence terminal on a highly modified branch ; female bracts much enlarged, the upper two or more times as large as the branch leaves and with modified areolation. (In some respect, the structure of the female branch and female bracts approaches stem and stem leaf anatomy, rather than branch and branch leaf anatomy.) Capsule spherical, eperistomate, dehiscing via an apical lid ; archesporium in the form of a hollow hemisphere. True seta not developed, stalk of fruit made up of gametophyte tissue (pseudopodium). Spores tetrahedral. Prothallus thalloid. Chromosome no. $n = 19 + 2m$; $38 + 4m$ (e.g. Holmen, 1955 ; Bryan, 1955).

Almost cosmopolitan but more or less confined to areas with 1200 mm mean annual rainfall and without a pronounced dry season (Map 1).


SPHAGNUM
Arctic Circle
Tropic of Cancer
Equator
Equator
Tropic of Capricorn
Antarctic Circle
180° Longitude 160° West
20° Meridian of 0° Greenwich 20°
140° Longitude 160° East
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The London Geographical Institute

MAP 1

Key to the *Sphagnum* species of tropical Asia

Cortical leucocysts of stem and branches normally with spiral fibrils (Figs 1, H; 2, B); branch leaves cucullate, dorsal apex appearing scabrid (Fig. 1, D); pseudolacunae invariably present on dorsal surface (Fig. 2, E)(Subgen. *Sphagnum*):

Cortical cells of stem with a single pore in the external wall (Fig. 4, C). Chlorocysts always exposed on the ventral surface of branch leaves . . . . . . *S. perichaetiale*

Cortical cells of stem with 2 – several pores in the external wall, at least in the majority of cells (Fig. 1, H) (if uniporose, then chlorocysts not reaching either surface of branch leaves):

Chlorocysts of branch leaves broadly triangular in transverse section, always widely exposed on the ventral surface (Fig. 2, E) . . . . *S. palustre*

Chlorocysts in transverse section oval, completely enclosed by adjacent leucocysts (Fig. 5, E) *S. magellanicum*

Cortical leucocysts never fibrillose; branch leaves truncate-dentate or mucronate at apex (Figs 9, E; 24, H), if apparently cucullate, then not scabrid and without pseudolacunae:

Branch leaves large, more than 3·0 mm long, sub-squarrose or patent, pseudolacunae invariably present on the *ventral* surface of branch leaves (Fig. 23, E); chlorocysts in section oval; commissural walls papillose . . . . *S. strictum*

Branch leaves various, never with pseudolacunae on the ventral surface (if present on the dorsal surface, then chlorocysts in section triangular or trapezoid); commissural walls smooth:

Branch leaves contracted at apex to an acute mucro (Fig. 24, H); leucocysts without fibrils and with a single pore in the apical angle (Fig. 24, E, F) (Subgen. Homophylla) *S. sericeum*

Branch leaves never mucronate; leucocysts fibrillose or, if efibrose, then multiporose (Subgen. *Isocladus*):

Leucocysts of branch leaves without fibrils:

Branch leaves 3·0 – 4·5 mm long; leucocysts with pores more or less confined to the cell-angles . . . . *S. efibrillosum*

Branch leaves 1·0 – 1·5 mm long; leucocysts with numerous pores over the whole dorsal surface (cell appearing reticulate) (Fig. 14) . . . . *S. novo-caledoniae*

Leucocysts of branch leaves always fibrillose:

Chlorocysts in transverse section triangular, trapezoid or rectangular, thin walled; pores various but never in uninterrupted series along the commissures:

Chlorocysts of branch leaves with much wider exposure on the *ventral* surface. Leucocysts strongly inflated dorsally; pseudolacunae usually present on dorsal surface (Sect. Acutifolia) . . . . *S. junghuhnianum*

Chlorocysts of branch leaves with much wider exposure on the *dorsal* surface (if exposed more or less equally on both surfaces, then upper branch leaves linear, more than 2·5 times as long as wide). Leucocysts not normally strongly inflated. Pseudolacunae never developed (Sect. Cuspidata):

Branch leaves of uniform length, markedly pentastichous, less than 2·5 times as long as wide. Stem leaves widely rounded or truncate at apex and appearing fimbriate (Fig. 18, C):

Stem leaves with leucocysts near apex fibrillose. Ventral surface of branch-leaf leucocysts with small pores not exceeding 5·0 µm diameter *S. novo-guineense*

Stem leaves efibrose throughout, rarely with incomplete fibrils in a few cells near apex. Ventral surface of branch-leaf leucocysts with pores exceeding 7·0 µm diameter . . . . *S. cuspidatulum*

At least the distal branch leaves long and narrow, appearing linear or subulate, more than 2·5 times as long as wide. Stem leaves more or less triangular, contracted above to a concave, subacute or *narrowly* truncate-dentate apex (Figs 15 ; 16) . . . . *S. cuspidatum*

All except a few basal branch leaves linear ; chlorocysts never completely immersed on the ventral surface (i.e. adjacent hyaline cells never with fused common wall) ; pores on ventral surface normally less than 6·0 μm diameter . . . . *S. cuspidatum* subsp. *cuspidatum*

A varying number of lower branch leaves short, resembling those of *S. cuspidatulum*, but distal leaves linear ; chlorocysts of basal leaves frequently immersed ventrally ; pores on ventral surface of lower branch leaves normally exceeding 7·0 μm diameter . *S. cuspidatum* subsp. *subrecurvum*

Chlorocysts in transverse section more or less oval or urceolate, with oval lumen and at least the anterior or posterior walls distinctly thickened (Figs 6, J ; 8, D). Dorsal surface of branch leaves often with numerous small pores arranged in series along commissures (Fig. 7, F) (Sect. Subsecunda) :

Ventral surface of branch leaves with numerous large, 12·0–18·0 μm, unringed pores (resembling those of *S. cuspidatulum*) ; dorsal surface without or with few pores and/or pseudopores . . . . *S. antarense*

Ventral surface of branch leaves without pores, or with small pores, 4·0–8·0 μm, resembling those of the dorsal surface ; dorsal surface normally with numerous pores and pseudopores :

Dorsal surface of branch-leaf leucocysts with rather large (*c.* 10·0 μm) pores ; many leucocysts with additional large free pores in the cell mid-line (Fig. 12, E). Chlorocysts slightly but distinctly displaced towards the ventral surface *S. ceylonicum*

Dorsal surface of branch-leaf leucocysts with small (*c.* 5·0 μm) pores confined to the commissures (spasmodically with a *very few* additional pores near the leaf apex). Chlorocysts central or more frequently slightly but distinctly displaced towards the dorsal surface :

Stem cortex basically two-layered (very rarely reduced locally to a single layer). Branch leaves large, more than 2·0 mm long, wide and obtuse. Pores not in uninterrupted series. Plants robust, resembling subgen. *Sphagnum* (Figs 9, 10) . . . . *S. robinsonii*

Stem cortex one-layered (only spasmodically two-layered locally). Branch leaves various, 1·0–2·0 mm long (rarely longer in aquatic states) ; pores usually in series along the dorsal commissures (occasionally replaced in part by pseudopores) (Pl. 39, D–E). Plants various but seldom as robust as subgen. *Sphagnum* :

Plants small and delicate. Branch leaves less than 1·2 mm long. Stem leaves resembling branch leaves, fibrillose to base. Leucocysts of branch leaves relatively short, less than five times as long as wide (Fig. 7) *S. ovatum*

Plants small to medium sized (if small then stem leaves fibrillose near apex only, not resembling branch leaves). Branch leaves (except sometimes in *S. subsecundum*) usually over 1·1 mm long. Leucocysts of branch leaves long and narrow, up to ten or more times as long as wide :

Mature plants isophyllous, usually with underlying crimson pigmentation. Stem leaves as long as, or longer than, branch leaves, fibrillose almost or quite to base. Fascicles usually closely set and more or less concealing the stem (Fig. 8) . . . . . *S. luzonense*

Mature plants heterophyllous, never with crimson pigmentation (normally orange-brown or greenish). Stem leaves shorter than branch leaves, fibrillose only in the upper half (typically only near apex). Fascicles usually rather distant, with distinct internodes visible (Fig. 6) *S. subsecundum*

Subgenus 1. *SPHAGNUM*

SPHAGNUM subgen. SPHAGNUM

Sphagnum sect. *Obtusifolia* Wils., Bryol. Brit. : 17 (1855), excl. parte.
Sphagnum B. *Heterophylla* Lindb. in Öfvers. K. VetenskAkad. Förh. Stockh. 19 : 134 (1862) excl. parte.
Sphagnum 7. *Cymbifolia* Schlieph. in Verh. zool.-bot. Ges. Wien 15 : 413 (1865), *nom. nud.*
Sphagnum sect. *Heterophylla* (Lindb.) Braithw. in Mon. microsc. J. 7 : 55 (1872).
Sphagnum A. *Palustria* Lindb. in Acta Soc. Scient. fenn. 10 : 263 (1872), *nom. nud.*
Sphagnum sect. *Cymbifolia* W. P. Schimper, Syn. Musc. Eur., ed. 2 : 847 (1876).
Sphagnum 6. *Cymbifolia* Lesq. & James, Man. Mosses N. Amer. : 21 (1884).
Sphagnum I. *Inophloea* Russow in Schr. Naturf.-Ges. Univ. Dorpat 3 : 27 (1887).
Sphagnum sect. *Platysphagnum* C. Muell. Hal.* in Flora, Jena 70 : 404 (1887).
Sphagnum subgen. *Inophloea* (Russow) A. LeRoy Andr. in Bryologist 14 : 72 (1911).
Sphagnum I. *Cuculifolia* Szafran in Acta Soc. Bot. Pol. 17 : 133, 136 (1946).

Type : *Sphagnum palustre* L.

Plants normally robust with a somewhat turgid aspect, pale green, ochraceous or with crimson pigments. Cortical cells of stem in 3–4 layers ; outer cells of cortex normally with spiral fibrils (occasionally undetectable in *S. perichaetiale*) and one or more large pores. Branch leaves large, rarely under 1·5 mm long, very concave ; leaf apex cucullate and usually appearing scabrid on the dorsal surface due to the resorption of the apical part of the leucocyst, the remainder projecting somewhat above the general leaf surface. Pseudolacunae always present, confined to the dorsal leaf surface and to the convergence of the basal and lateral angles of adjacent hyaline cells.

About 10 species, the distribution of the subgenus more or less paralleling that of the genus.

Although some species of subgenus *Rigida* or section *Subsecunda* may closely resemble the present group in the field, under the microscope no such confusion is likely. Structural features most closely approximate to section *Acutifolia* but the leaf form and cortical fibrillation are quite distinct.

Opinions vary as to the 'advanced' or 'primitive' nature of subgenus *Sphagnum*. Structurally its species are the most complex of the genus, yet many of its unique features are regarded by some authors as primitive (in particular, the cortical fibrils which, however, should not be interpreted as homologues of those in the leaf leucocysts). The wide variation in form and position of the chlorocysts is probably indicative of the antiquity of the subgenus, but its age relative to the other subgenera remains unestablished (see discussion under heading 'Phylogeny and Evolution', pp. 366–367).

1. ***Sphagnum palustre*** L., Sp. Pl. 2 : 1106 (1753).

1a. Subsp. ***palustre***. Not present in our area. (Text-fig. 2, F.)

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*This seems to be the most appropriate way to cite Karl August Friedrich Wilhelm Müller (1818–1899), who normally called himself in his published works Carl Müller or Carolus Müeller Halensis, and who needs to be distinguished from Carl Müller (1817–1870), editor of Walper's Annales, C. A. E. Müller (1855–1907) of Berlin, author of the general account of the Musci in the Pflanzenfamilien, and Karl Müller (1881–1955) of Freiburg, the hepaticologist.

1b. Subsp. ***pseudocymbifolium*** (C. Muell. Hal.) A. Eddy stat. nov. (Text-figs 1–2; Plate 37, A–E.)

S. pseudocymbifolium C. Muell. Hal. in Linnaea 38 : 547 (1874).
S. assamicum C. Muell. Hal. in Flora, Jena 70 : 411 (1887).
S. siamense H. N. Dixon in J. Siam Soc. 9 : 3 (1933).

Habit and size of the subgenus; pale whitish green varying to dark brownish. Stem about 1·0 mm diameter; cortical cells in 3–4 layers, fibrillose and with (1–)2–4(–6) pores; central cylinder dark brown or blackish. Branches 4–5 in a fascicle, dimorphic; two spreading branches 10–15 mm long or more; 2–3 pendent branches variable, usually shorter, pale, caudiform. Branch cortex fibrillose; cortical leucocysts mostly with a single pore in the outer wall. Stem leaves rectangular, lingulate to spathulate, 1·4–2·0 mm long, 0·9–1·1 mm wide, unbordered; apex widely rounded-truncate, margin hyaline, ephemeral or appearing eroded or fimbriate; fibrillose at least in the upper third, sometimes almost to base; sometimes with considerable resorption of the dorsal wall of the leucocysts. Branch leaves concave, widely ovate, appearing scabrid on dorsal surface near apex; apex markedly cucullate; normal leaves about 1·5–2·0 mm long, 1·35–1·45 mm wide (somewhat smaller than average subsp. *palustre*); border with resorption furrow. Leucocysts wide, 25–35 μm, strongly inflated dorsally, slightly so or almost plane ventrally; ventral surface, except 4–6 marginal rows, eporose or with a single, usually unringed, pore in the apical angle; dorsal surface with 1–3 normal pores per cell, more or less confined to the cell angles; pores more numerous in a wide zone (4–6 cells width) near the margins, large, ringed, about 12–20 μm diameter; triple pores (pseudolacunae) present but commonly opening wide-mouthed and therefore hardly distinguishable from normal pores in surface view of the dorsal face of branch leaves. Chlorocysts in section equilateral or broadly isosceles triangular, thin-walled, widely exposed on the ventral surface but just reaching dorsal surface and often appearing immersed due to the adjacent hyaline cells occluding the dorsal 'apex'.

Fertile material not seen but unlikely to differ from that of subsp. *palustre* to any significant degree.

Chromosome number not known. Diploid (Bryan, 1955; Holmen, 1955) numbers have been reported for gametophytes of subsp. *palustre* (i.e. n = 38).

Almost confined to continental tropical and subtropical Asia south of the Himalaya; known also from Taiwan and possibly occurs in South Japan (Maps 2 & 3).

INDIA: Sikkim: *J. D. Hooker 1289* (BM, type collection). Catsuperri Lake, *Hooker & Thomson 1292*. Assam: *Rankin & Pritzlik M. 16* (BM).

BHUTAN: Jongsa *Griffith s.n.* (BM; NY).

NEPAL: Chiline Khola *O. Polunin M130* (BM).

THAILAND: Udawn, *Kerr 80* (BM, holotype of *S. siamense* Dix.); *Kerr 428, 568* (BM). Kao Kradeng, *Akun 568* (BM, collector's name possibly mistranscribed on label). Udawn, *A. Touw 10855, 10859, 11092* (L). Poo Kradeng, *Thai–Danish Botanical Studies Expedition* (*TDBS*): several collections including *TDBS 6402, 4640* (C; L). *Smitinand 1158* (L).

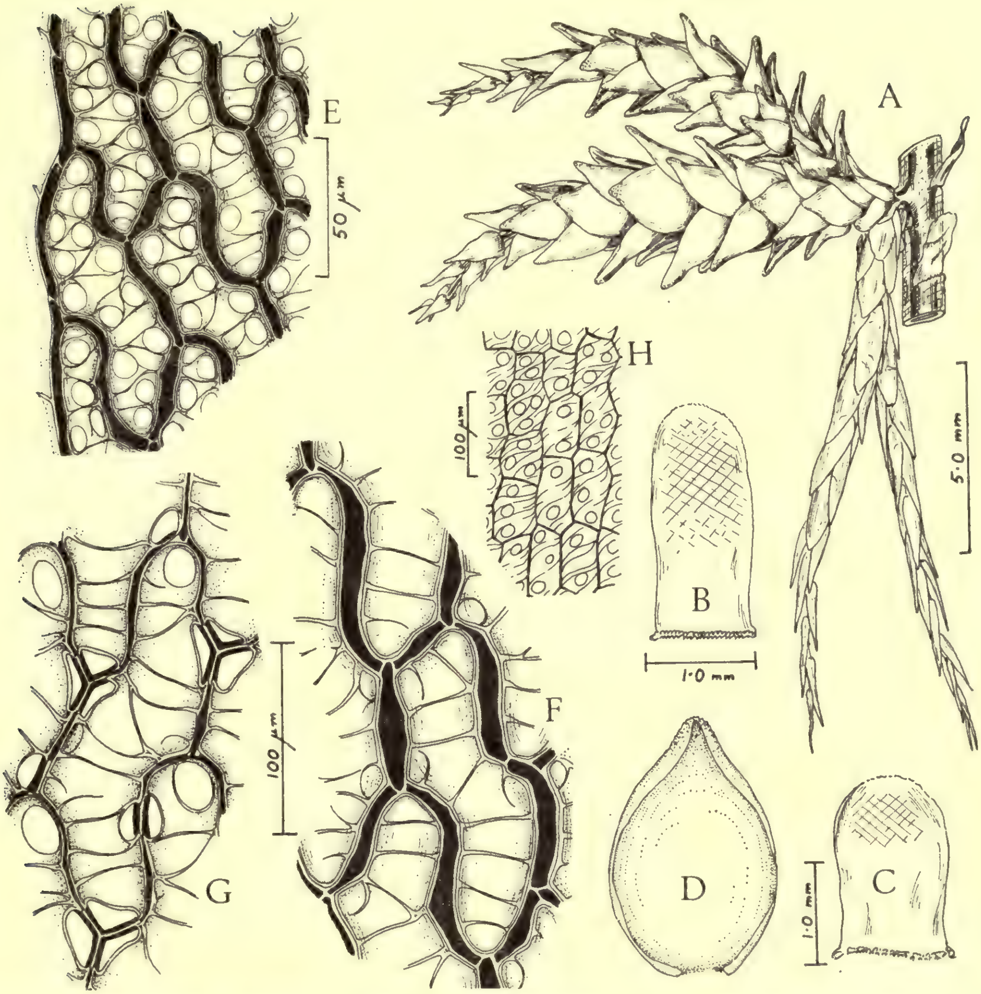


FIG. 1. *Sphagnum palustre* L. subsp. *pseudocymbifolium* (C. Muell. Hal.) A. Eddy: A, branch fascicle; B, C, stem leaves; D, branch leaf; E, mid-ventral margin of branch leaf; F, ventral surface of branch leaf; G, dorsal surface of branch leaf; H, outer face of stem cortex. (All except C drawn from *Hooker 1289*; C drawn from *Kerr, 80*.)

CHINA: Yunnan, *Handel–Mazzetti 7912* (BM).

TAIWAN: Taitum, *Faurie 213, 214* (BM).

Sphagnum palustre subsp. *pseudocymbifolium* is distinguished from subsp. *palustre* only by the characteristic form of the chlorocysts of the branch leaves. These, in transverse section, resemble in shape those of *S. imbricatum* Russ. but are quite smooth (Fig. 2, E). This character was regarded as inconsequential by LeRoy Andrews (1951), and later by Hansen (1961). While I do not support the views of Gangulee (1969), who maintains Müller's species in his treatment of the Indian *Sphagna*, I find the character sufficiently constant over the range indicated to warrant the distinction of this plant from subsp. *palustre*. It is only in China and Japan that intermediate forms have been collected, forms which cannot be confidently identified with one or the other subspecies. Possibly subsp. *pseudocymbifolium* evolved in the east of the range of the aggregate, migrating westwards and becoming isolated by the Himalayan massif.

Forms of *S. palustre* from comparable situations in North America do not share the characters of the tropical Asiatic plant, which argues against the latter being no more than a modification due to climate.

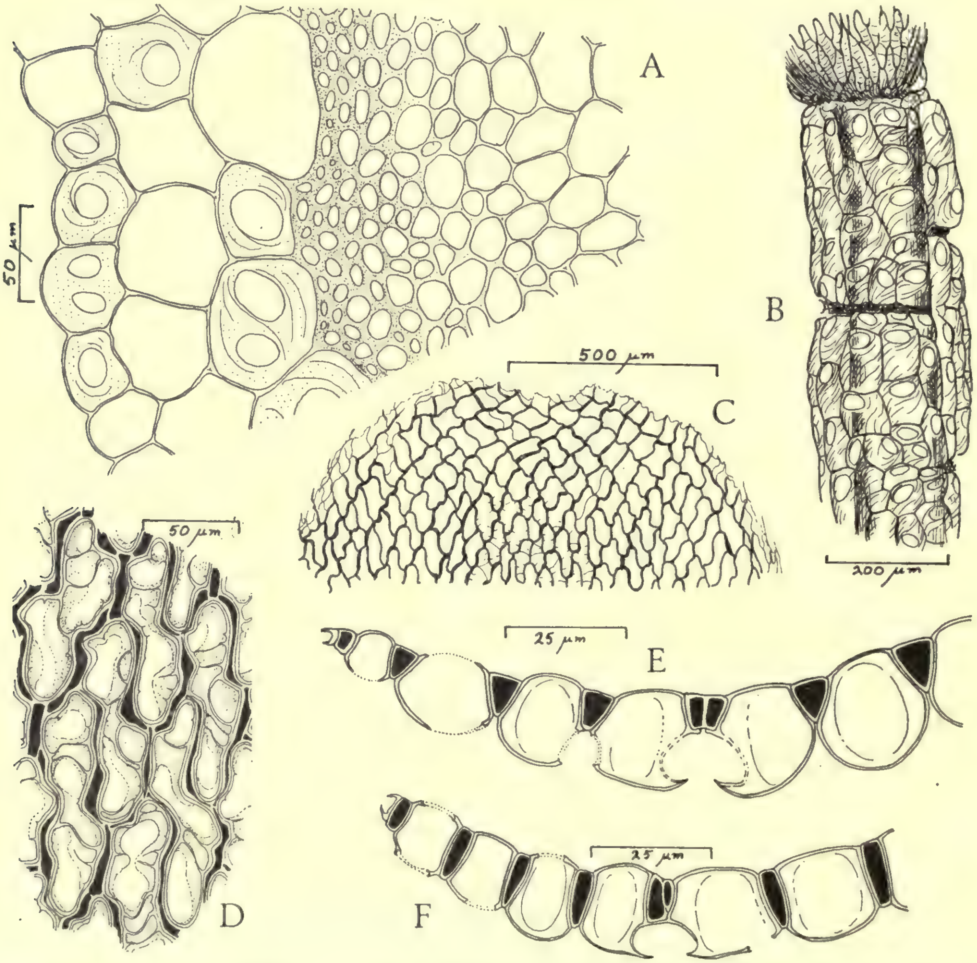
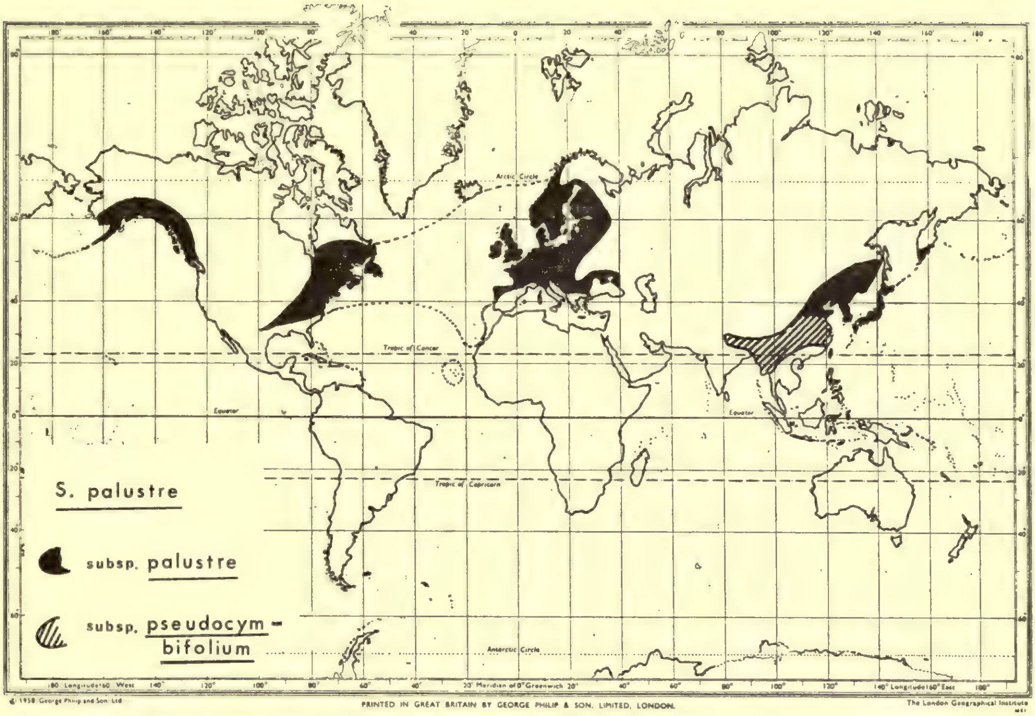


FIG. 2. *Sphagnum palustre* L. subsp. *pseudocymbifolium* (C. Muell. Hal.) A. Eddy: A, transverse section of stem; B, part of branch, defoliated; C, apex of stem leaf; D, dorsal surface of stem leaf, near leaf apex; E, transverse section of branch leaf. *Sphagnum palustre* L. subsp. *palustre*: F, transverse section of branch leaf. (A–E drawn from *Hooker 1289*; F from a British specimen, *Eddy s.n.*)


S. palustre
subsp. palustre
subsp. pseudocymbifolium
Arctic Circle
Tropic of Cancer
Equator
Tropic of Capricorn
Antarctic Circle
180 Longitude 160 West
20° Meridian of 0° Greenwich 20°
140° Longitude 160° East
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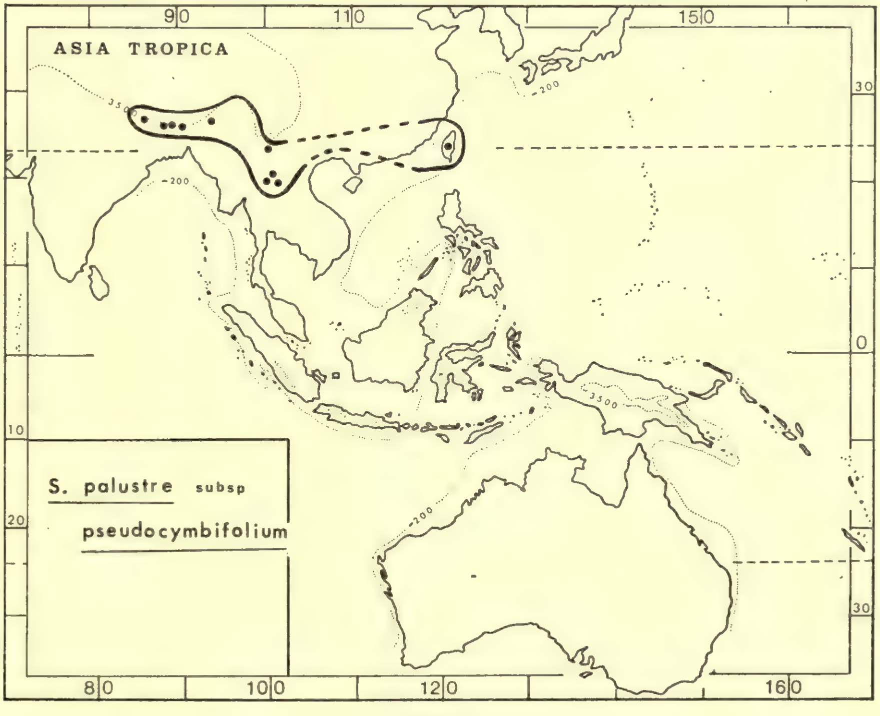
MAP 2


ASIA TROPICA
90
110
150
30
0
10
20
30
80
100
120
160
3500
200
S. palustre subsp pseudocymbifolium

MAP 3

2. *Sphagnum perichaetiale* Hampe in Linnaea 20 : 66 (1847). (Text-figs 3 & 4).

S. erythrocalyx auct. non Hampe 1848.
S. negrense Mitten in J. Linn. Soc., Bot. 12 : 624 (1869).
S. peruvianum Mitten, tom. cit. : 625 (1869).
S. beccarii Hampe in Nuovo G. bot. ital. 4 : 278 (1872).
S. guyonii Warnst. in Bt. bot. Mschr. 2 : 17 (1884).
S. cymbifolium var. *ludovicianum* Renauld & Cardot apud Cardot in Bull. Soc. r. Bot. Belg. 26, Mém. : 42 (1887).
S. puiggarii C. Muell. Hal. in Flora, Jena 70 : 409 (1887).
S. wrightii C. Muell. Hal., tom. cit. : 411 (1887).
S. vitjianum W. P. Schimper ex Warnst. in Hedwigia 30 : 144, t.14 f.8, t.21 f.1 (1891).
S. antillarum Warnst., tom. cit. : 147, t.15 f.11, t.21 f.o (1891).
S. brachybolax C. Muell. Hal. ex Warnst., tom. cit. : 150 (1891).
S. griffithianum Warnst., tom. cit. : 151, t.16 f.19, t.22 f.x (1891).
S. paucifibrosum Warnst., tom. cit. : 152, t.16 f.20a, b, t.22 f.y (1891).
S. balfourianum Warnst., tom. cit. : 153, t.17 f.21, t.22 f.z (1891).
S. ludovicianum (Renauld & Cardot) Warnst., tom. cit. : 161, t.18 f.26, t.23 f.gg (1891).
S. arbogastii Renauld & Cardot in Bull. Soc. r. Bot. Belg. 32(2) : 8 (1893), 'Arbogastii'.
S. carneum C. Muell. Hall & Warnst., tom. cit. : 170 (1897).
S. brachycladum C. Muell. Hal. ex Warnst., tom. cit. : 170 (1897).
S. subtursum C. Muell. Hal. ex Warnst., tom. cit. : 171 (1897).
S. ouropretense C. Muell. Hal. & Warnst. apud Warnst., tom. cit. : 172 (1897).
S. kegelianum C. Muell. Hal. ex Warnst., tom. cit. : 175 (1897).
S. sintenisii C. Muell. Hal. in Hedwigia 37 : 219 (1898), *'Sintenisi'* – Warnstorf in Bot. Zbl. 76 : 387 (1898).
S. heterophyllum Warnst. apud Ule in Bot. Jb. 27 : 254 (1899).
S. subbrachycladum C. Muell. Hal. ex Warnst. apud Ule, tom. cit. : 255 (1899).
S. suberythrocalyx C. Muell. Hal. ex Warnst. apud Ule, tom. cit. : 256 (1899).
S. grandifolium Warnst. in Bot. Zbl. 82 : 33 (1900).
S. brevicaule Warnst. in Hedwigia 39 : 108 (1900).
S. pauciporosum Warnst., tom. cit. : 109 (1900).
S. geheebii Warnst. in Magy. bot. Lap. 1 : 44 (1902).
S. paranae Warnst. in Allg. bot. Z. 11 : 97 (1905).
S. macroporum Warnst., tom. cit. : 98 (1905).
S. submedium Warnst. in Beih. bot. Zbl. 20(2) : 134 (1906).
S. pauloense Warnst., tom. cit. : 136 (1906).
S. santosense Warnst., tom. cit. : 137 (1906).
?*S. leratianum* Paris & Warnst. apud Warnst. in Pflanzenreich 51 (= Sphagnologia Universalis) : 476 f.51A (1911), 'Le Ratianum'.
S. earlei Warnst., tom cit. : 449 (1911).
S. japonicum var. *philippinense* Warnst., tom. cit. : 520 (1911).
S. marlothii Warnst., tom. cit. : 471 (1911).
S. biforme Warnst., tom. cit. : 493, fig. 84E (1911).
S. orgaosense Warnst., tom. cit. : 500, fig. 81D (1911).
S. glaucovirens Warnst., tom. cit. : 501, fig. 81E (1911).
S. allionii Warnst., tom. cit. : 502, fig. 82B (1911).
S. bahiense Warnst., tom. cit. : 502, fig. 81F (1911), excl. var. *sincorae*.
S. tijucae Warnst., tom. cit. : 503, fig. 79D (1911).
S. derrumbense Warnst., tom. cit. : 508 (1911).
S. discrepans Warnst., tom. cit. : 510, fig. 85 (1911).
S. huntii Warnst., tom. cit. : 521 (1911).
S. fleischeri Warnst., in Hedwigia 57 : 77 (1915).
S. kelantanense H. N. Dixon in Gdns' Bull. Straits Settl. 4 : 2 (1926), ***nom. nud.***

S. attenuatum H. N. Dixon in J. Bot. Lond. 79 : 57 (1941).
S. roseotinctum Anne Johnson in Gdns' Bull., Singapore 17 : 320, fig. 1c – e, fig. 2a. (1959).
S. holttumii Anne Johnson, loc. cit. : fig. 1h, i, fig. 2b.

Plants extremely variable in size, colour and habit ; usually moderately robust, pale greenish to fairly deep brown or yellow-brown, not infrequently tinged with crimson or whole plant suffused red. Stems 0·8 – 1·2 mm diameter, internal cylinder brownish to dark reddish-brown to almost black ; cortex easily separable, in 2 – 4 layers ; outer cells about 40 μm wide, most of them having a single large pore on the

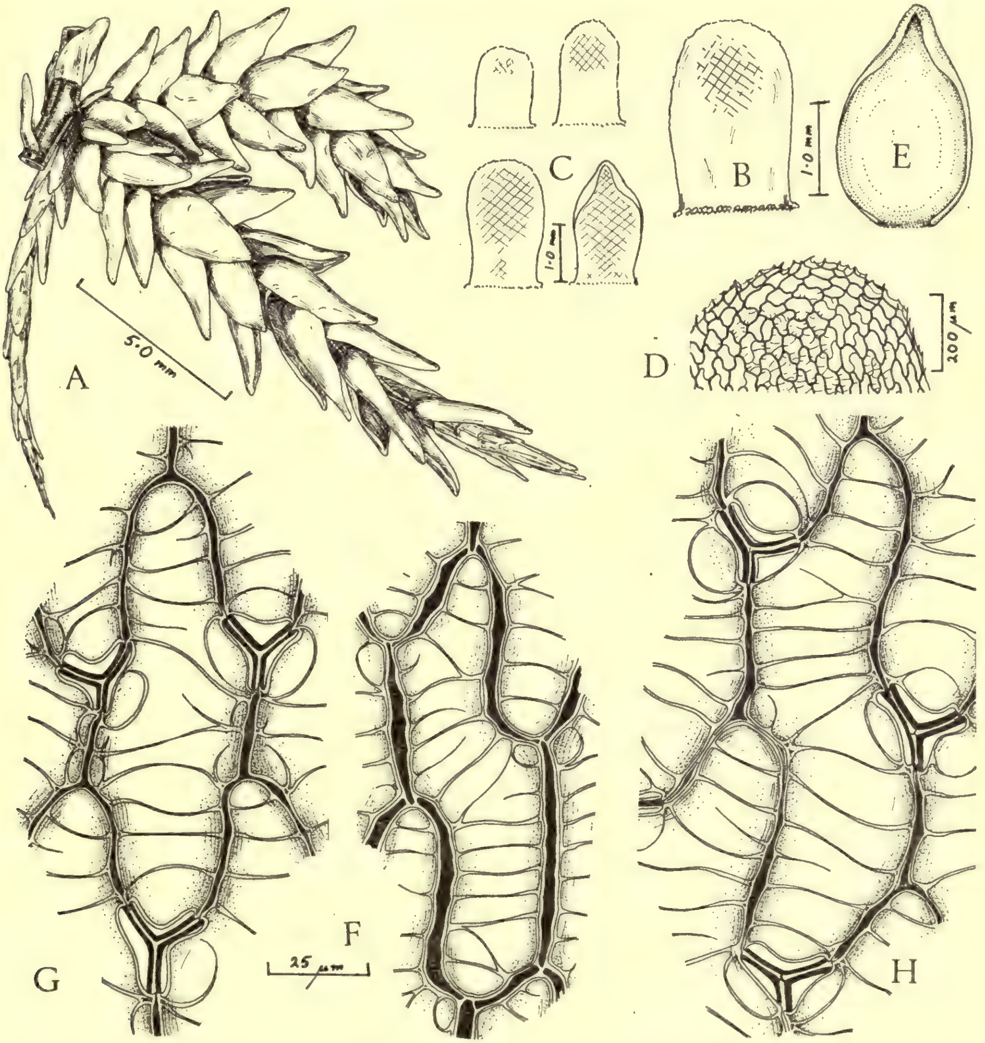


FIG. 3. *Sphagnum perichaetiale* Hampe : A, branch fascicle ; B, stem leaf ; C, range of stem-leaf morphology ; D, apex of stem leaf (heterophyllous form) ; E, branch leaf ; F, ventral surface of branch leaf ; G, H, dorsal surface of branch leaf. (A, B, D, E, F, G drawn from *Beccari 15* ; H from *Eddy 213* ; C from various Asiatic specimens.)

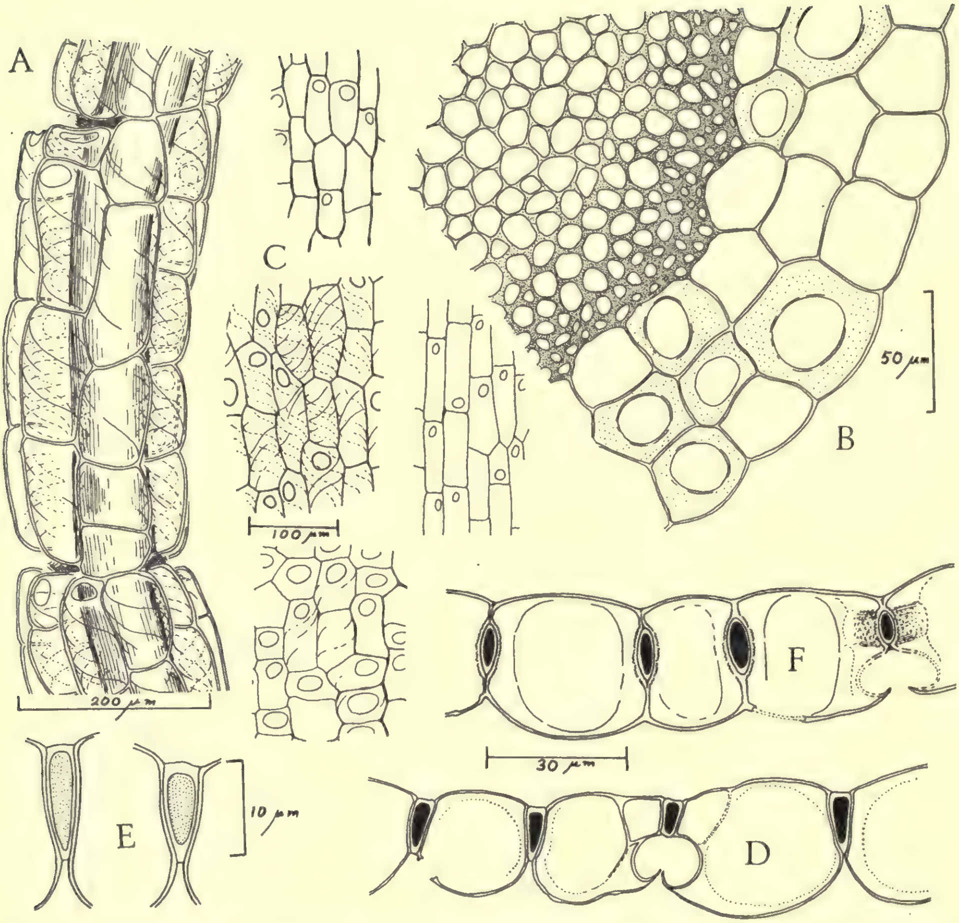


FIG. 4. *Sphagnum perichaetiale* Hampe: A, defoliated branch; B, transverse section of stem; C, variation in cortical fibrillation; D, transverse section of branch leaf; E, transverse sections of chlorocysts; *Sphagnum erythrocalyx* Hampe: F, transverse section of branch leaf. (A, B, D drawn from *Beccari 15*; C, E from various Malaysian specimens; F from the holotype of *S. erythrocalyx*.)

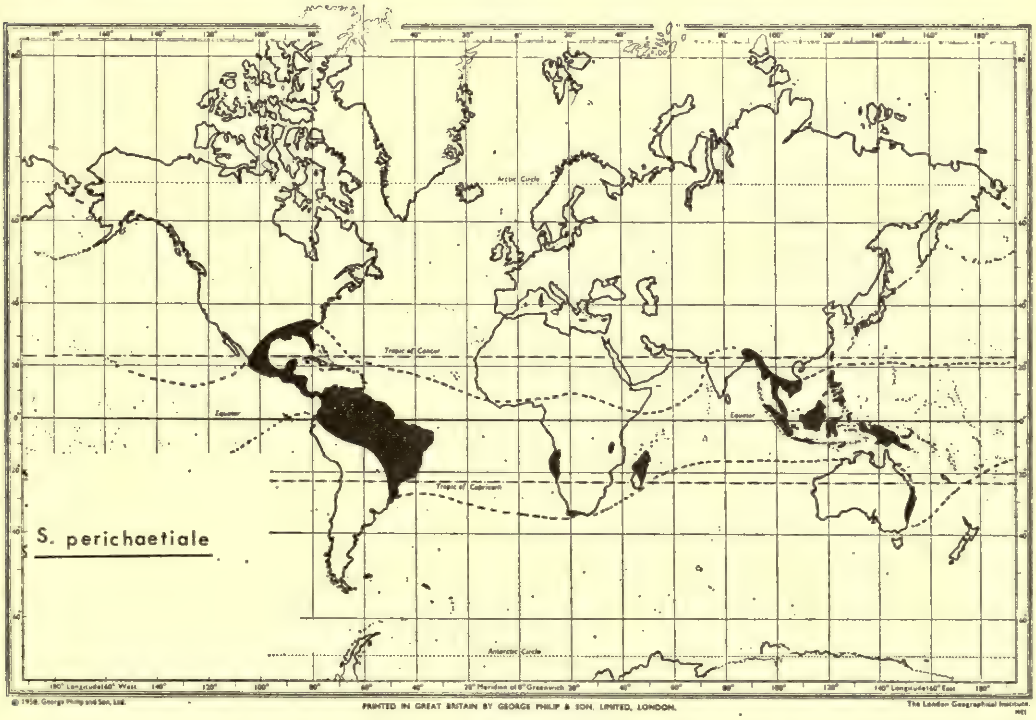
outer face (extremely rarely the occasional cell near a branch insertion may have a second pore, but this condition has not been seen in Asiatic material); cortex fibrillose, often weakly so, or efibrose (Fig. 4, C). Branches usually three or four in a fascicle, dimorphic; 1–3 spreading branches 7·0–1·5 mm long, blunt and somewhat tumid; 1–2 pendent branches pale and weak, caudiform. Cortical leucocysts of branches foraminate, usually fibrillose but often very faintly so, more or less uniform. Stem leaves very variable, from shortly rectangular and efibrose through a gradation of states to complete isophylly, (1·2–)1·6–2·5(–3·0) mm long, about 1·0–1·3 mm wide (Fig. 3, C). Branch leaves (Fig. 3, E) typical of the subgenus, very concave, cucullate, more or less scabrid dorsally at apex (sometimes less so than in other species of the subgenus); (1·8–)2·0–3·0 mm long. Simple pores more or less confined to the

2–3 intramarginal rows of leucocysts, few or absent over the rest of the leaf surface, large, 10–20 μm diameter, ringed; pseudopores few to numerous on one or both surfaces; pseudolacunae in surface view with relatively narrow, three-armed aperture in normal leaves (Fig. 3, G; Pl. 37, F); leucocysts strongly inflated dorsally, much less so ventrally; Chlorocysts narrow, up to 5·0 μm wide, in section variable, typically somewhat urceolate or triangular-oval, incrassate with the anterior wall thickened and with slightly rounded lumen, frequently more or less trapezoid and, in aquatic forms, thin-walled (then strongly resembling *S. palustre* subsp. *palustre*), just reaching or very narrowly exposed on the dorsal surface (often appearing enclosed due to proximity of adjacent leucocysts, but the latter never having a fused common wall), with 4·0–5·0 μm ventral exposure.

Dioecious? Very rarely fertile except locally in America, no fruiting material recorded from Asia. Male bracts resembling the branch leaves. Female bracts large, the inner up to 4·0–5·0 mm long, fibrillose in the upper part, elsewhere efibrose and near insertion with uniformly prosenchymatous tissue. Spores not seen.

Chromosome number of 19+2m reported by Bryan (1955) for North American material (as *S. erythrocalyx* auct.).

Irrigated rocks and acid organic and inorganic substrates in open to semi-shaded regions rather more confined to subaquatic habitats than other species of subgenus *Sphagnum* (Maps 4 & 5).


S. perichaetiale
Arctic Circle
Tropic of Cancer
Equator
Equator
Tropic of Capricorn
Antarctic Circle
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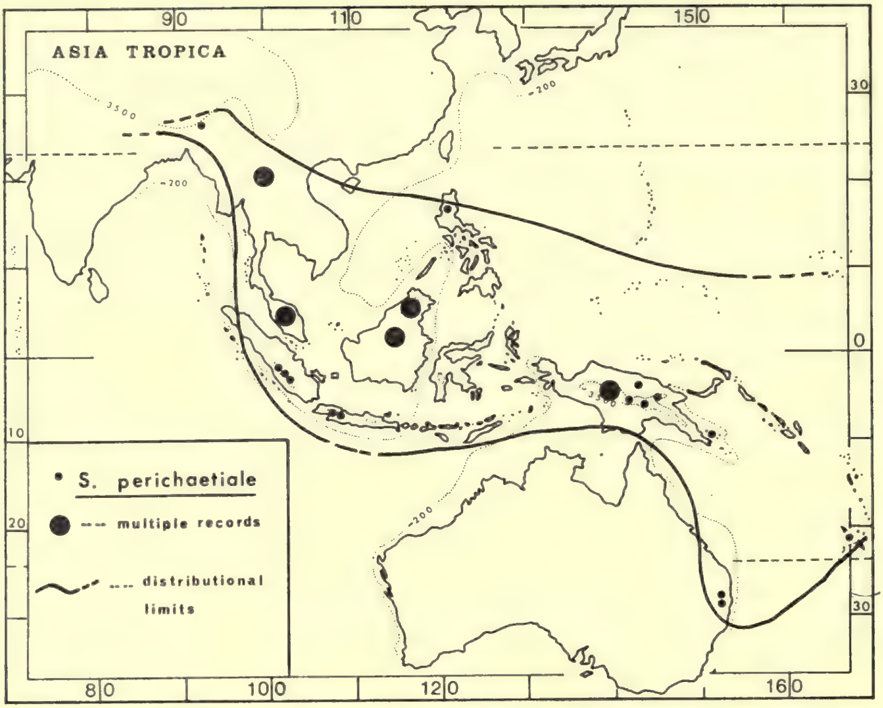
MAP 4


ASIA TROPICA
90
110
150
30
0
10
20
30
80
100
120
160
3500
200
S. perichaetiale
multiple records
distributional limits

MAP 5

Asia and Indo-Pacific :

INDIA : Sikkim, *Griffith* (BM, isotype of *S. griffithianum*).

VIETNAM : Dalat, *Nguyen van Thuy 102/A3*(C).

CAMBODIA : *Smitinand & Abbe 6452, 6499* (BM).

THAILAND : Udawn, *Hansen et al., TDBS 2288, 6403, 6440, 6441* (C ; L) ; *Touw 11006, 11089* (L).

MALAYA : Kedah, *Spare 1430, 1439* (BM ; SING), *2386, 2388, 2844, 2872* (BM) ; *Holttum 20906* (holotype of *S. holttumii*, SING), *14882b, 20908, 20909, 20910* (BM ; SING) ; *Robbins 3699* (BM) ; *Kadir 19771* (SING) ; *Evans & Gordon 1097* (BM). Kelantan, *Nur 12244* (SING, type collection of *S. roseotinctum*). Pahang, *Holttum 20916, 20919, 23300* (BM ; SING) ; *Henderson 17877c* (L). Johore, *Corner 23207* (BM).

SUMATRA : Atjeh, *Van Steenis 4017* (BM ; L). Lubuh Bangku, *Meijer 9664* (L). Pajakumbuh, *Meijer 6420, 6049* (L).

JAVA : G. Salak, *Teysmann* (L, 2 specimens). Banca, *Van Diest* (L).

BORNEO : Sarawak, *Beccari 15* (BM, holotype of *S. beccarii*, Herb. Hampe), *18, 26* (BM). Bei Kenepei, *Teysmann sn* (BO, isotype of *S. pauciporosum* ; also distributed in Fleischer, Musc. Arch. Ind. no. 51). G. Lambia, *Haviland & Hose* (BM, holotype of *S. attenuatum* Dix. ms.). Dulit Ridge, *Oxford Expedition (1932)*

2179, 2184 (BM). Santubong, *Richards 5701, 5698* (L). Kinabalu, *Meijer 10954, 11028*, *12246* (L); Anderson *15695* (L).

PHILIPPINES: Luzon, *Bur 16996* (BM, type collection of *S. japonicum* var. *philippinense*).

NEW GUINEA: West Irian: Arfak Mts, *Sleumer & Vink 4343, 4348* (L); *Van Royen & Sleumer 7190* (L). Star Mts, *Van Zanten 351, 444* (BM; GRO). New Guinea: Edie Creek, *Eddy 1a, 213, 224* (BM); Finisterre Range, *Eddy 1150* (BM). Mt Kaindi, *Van Zanten 68310, 68314, 68308*, (GRO). Western Highlands, *Walker ANU 506* (BM). Amanab, *Argent s.n.* (BM). Milne Bay, *Cruttwell 1340* (L). Eastern Highlands, *Sleumer 4610* (L). D'Entrecastreaux, *Brass 25666* (L).

NEW CALEDONIA: Bourail, *Le Rat* (BM, isotype of *S. leratianum*). Plaines des Lacs, *Franc* (L).

FIJI: Viti, *Hooker 65* (BM, Herb. Schimper, holotype of *S. vitjianum*); *Graeffe 37* (BM).

Australasia:

AUSTRALIA: New South Wales, *Watts 3078* (BM; NSW; type collection of *S. grandifolium*), *3081, 4021, 4134, 4208* (NSW); Lake Medlow, *Constable M 11066* (NSW).

Africa:

SOUTH AFRICA: Table Mountain, *Taylor 1105* (BM); *Esterhuysen 15839* (BM); *Pillars 4280* (BM).

ANGOLA: *Gossweiler 2804* (BM).

MADAGASCAR: St Marie, *Arbogast s.n.* (BM, isotype of *S. arbogastii*).

MAURITIUS: *Balfour s.n.* (BM; NY; isotypes of *S. balfourianum*).

America, South and Central:

PERU: *Spruce 1512* (BM, isotype of *S. peruvianum*).

BRASIL: *Beyrich s.n.* (BM, Herb. Hampe, holotype of *S. perichaetiale*); *E. Ule 290* (*S. brunnescens* fid. Warnstorf); *E. Ule 98* (BM, *S. brachybolax* fid. Warnstorf); *E. Ule 239* (BM, as *S. heterophyllum*), *137, 413* (BM, as *S .puiggarii*); *Döring s.n* (BM, Herb. Hampe); *Spruce 1507, 1508, 1510* (BM, including type collection of *S. negrense*); *Dusen 510* (BM, *S. brachycladum* fid. Warnstorf); *Schniffner 832, 833, 835* (BM, as *S. pauloense*); *Schiffner 233, 545* (BM, as *S. santosense*); *Schiffner 969, 9614* (BM, as *S. glaucovirens*).

ECUADOR: *Allioni 124* (BM, isotype of *S. derrumbense*), *s.n.* (BM, isotype of *S. allionii*).

PUERTO RICO: *Sintenis s.n.* (BM, isotype of *S. sintenisii*); *Underwood & Griggs 949* (BM).

CUBA: *Wright s.n.* (BM).

NORTH AMERICA: New Jersey, *Le Roy Andrews s.n.* (as *S. erythrocalyx*); *Eaton & Faxon, exsicc. 171, 172* (BM, as *S. ludovicianum*). Alabama, *Mohr s.n.* (BM). Florida, *Conard 58-1b* (BM); *Koch 7233* (BM); *Papp s.n.* (BM); *Gray s.n.* (BM).

S. perichaetiale favours montane areas within the tropics with high rainfall more or less throughout the year and is most abundant where oceanic influence is strongest. The paucity of material from the African mainland is due, no doubt, to the 'continental' nature of its climatic regimes. In the field there is little in the appearance of the plant to distinguish it from other species of the subgenus. It may be quite strongly red-pigmented, resembling *S. magellanicum*, or pale, resembling *S. palustre*. The former species is confined, within our area, to northern India and the latter to continental Asia. *S. perichaetiale* is readily distinguished from either by its uniporose cortical leucocysts and the shape and disposition of its chlorocysts.

Warnstorf has been frequently criticized for the multiplicity of names which he applied to the various forms of this species. It is of interest to note that he seems to have changed his approach at least once, and some of the names reinstated in his *Sphagnologia* he had himself previously reduced.

Temperate species of subgenus *Sphagnum* show considerable stability of form, but *S. perichaetiale*, a truly tropical species, is remarkable for its variation. Extreme forms often show so little resemblance to one another that early authors understandably regarded them as not conspecific. Even so, the characters upon which Warnstorf based his species are often scarcely more than trivial modifications, the sum of which represent a more or less continuous range of variation. Local populations may show a tendency to produce one form in favour of others, but in the main geographical strongholds of the species, tropical America and tropical Asia, there is hardly to be found a form in one which is not exactly paralleled in the other.

Hampe (1847, and in C. Müller, 1849) subscribed to the view that new species of *Sphagnum* should be based, as in other mosses, on fruiting characters. His descriptions of *S. perichaetiale* and *S. erythrocalyx* (in C. Müller, 1849) are both based on the morphology of the female bracts. It is now recognized that such characters are of little value in distinguishing species. Hampe's detailed account does, however, provide useful confirmation of his selection of holotypes in the herbarium. In the absence of detailed vegetative description, and largely on the basis of a specimen in Warnstorf's herbarium, Andrews reduced *S. perichaetiale* to *S. erythrocalyx*. There are two reasons why the epithet *erythrocalyx* cannot be applied to the Asiatic species. As Isoviita (1966) has already indicated, *S. perichaetiale* was, although inadequately diagnosed, validly published in 1847, thus antedating *S. erythrocalyx*. Furthermore, the holotypes (both in BM) represent quite different taxa. The morphology of the stem cortex and the branch leaves of *S. erythrocalyx* very closely resembles that of *S. magellanicum* Brid. but it differs in the papillosity of its commissural walls (Fig. 4, F). The holotype of *S. perichaetiale*, on the other hand, is a fair representative of the pan-tropical species described above. Andrews (1915) refers to the type collection, having been sent a BM specimen by Gepp. In view of his conclusions one can only assume that the material sent was not one of the fertile stems, upon which Hampe based his description.

LeRoy Andrews distributed the American synonyms between *S. palustre* L. and *S. erythrocalyx* (= *S. perichaetiale*). It would seem that he did this on the basis of the chlorocysts, as seen in section. There is no evidence that *S. palustre* occurs anywhere in the southern hemisphere.

The New Caledonian plant (*S. leratianum*) is of particular interest. A note against the isotype in the herbarium (BM) implies that Andrews, in a communication to H. N. Dixon, considered it to be merely one more synonym of *S. perichaetiale*. Later (Andrews, 1951), however, he reduced it to the Australasian *S. cristatum* Hampe. The isotype seems to fit within the range of form of *S. perichaetiale*, at least in the more important stem and chlorocyst morphology. Later collections (*Franc*, 1911) more closely approach *S. cristatum*. Further material is needed for study before a final decision is reached, but it is possible that this particular form indicates a link between the Australasian and Asiatic species.

3. ***Sphagnum magellanicum*** Bridel: Muscol. recent. 2(1): 24, 233, t.5 f.1 (1798). (Text-fig. 5.)

S. medium Limpricht in Bot. Zbl. 7: 313 (1881).

Plants robust, usually forming extensive mats or hummocks, nearly always with crimson pigments present except in dense shade, often the whole plant deep vinous

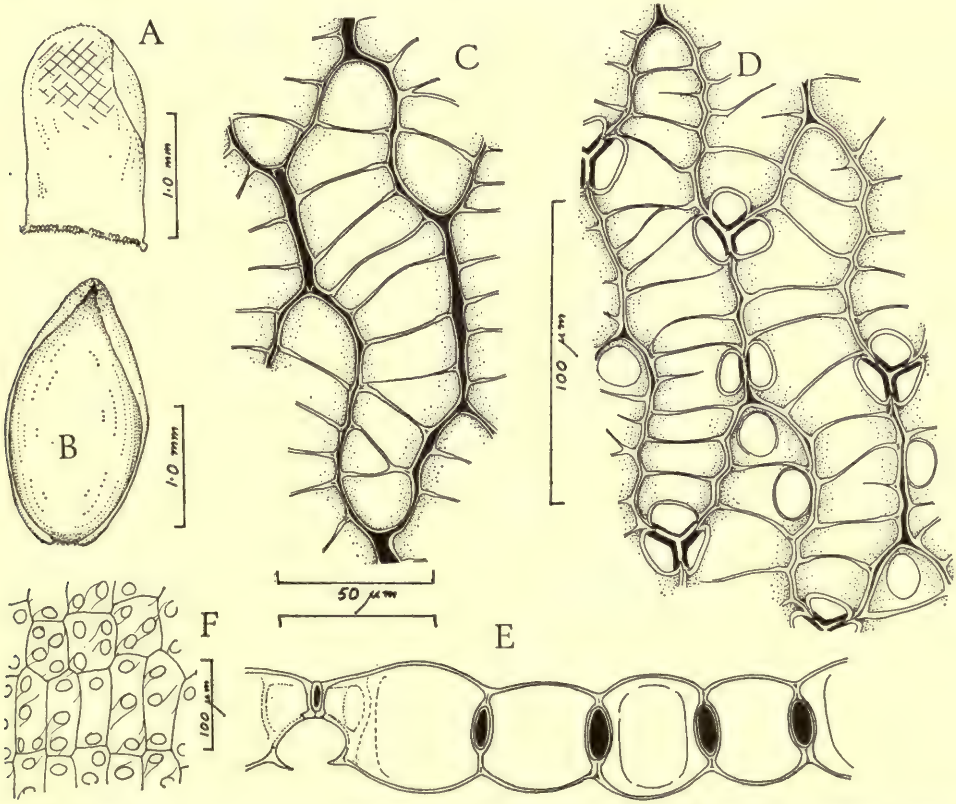
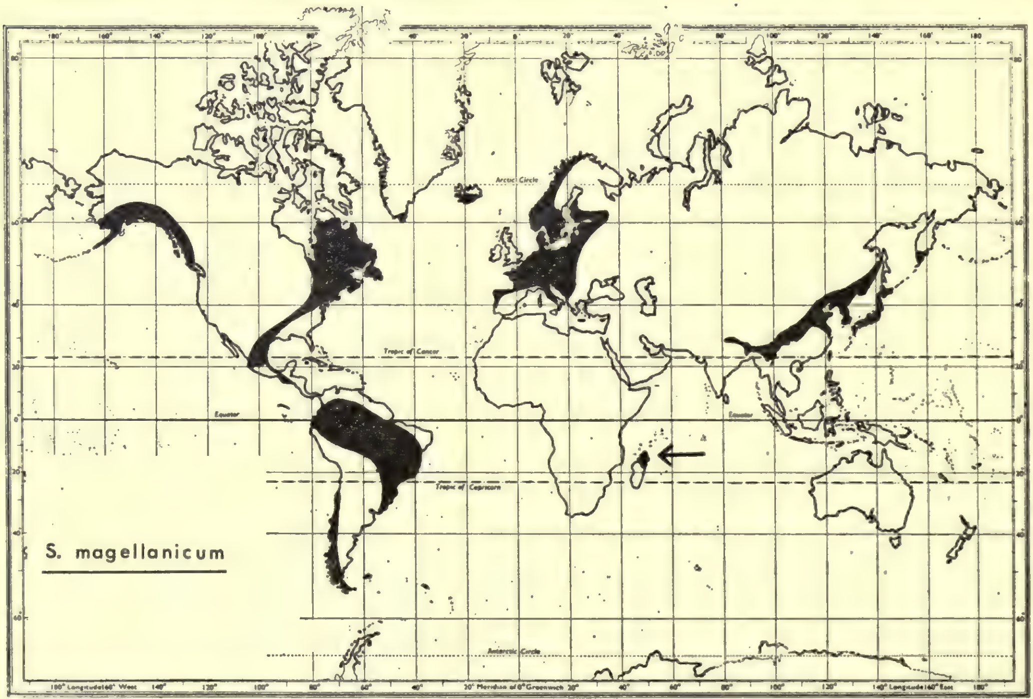


FIG. 5. *Sphagnum magellanicum* Bridel: A, stem leaf; B, branch leaf; C, ventral surface of branch leaf; D, dorsal surface of branch leaf; E, transverse section of branch leaf; F, outer surface of stem cortex. (All drawn from *Hooker 1283*.)

red. Stems to 1·2 mm diameter ; cortical cells in 3–4 layers, the outermost of which have (1–)2–4 or more pores per cell and usually distinct spiral fibrils ; central cylinder dark red-brown. Fascicles with (3–)4–5 branches which are strongly dimorphic ; spreading branches up to 20 mm long, usually blunt but sometimes more or less tapering ; pendent branches terete, pale, attenuated, more or less appressed to the stem. Stem leaves lingulate or spathulate, the apex widely rounded or truncate, ephemeral, hyaline or eroded and more or less fimbriate, (1·3–)1·6–2·1 mm long, 0·8–1·2 mm wide, fibrillose in the upper part and with numerous resorption gaps. Branch leaves typical of the subgenus, large, concave, 1·8–2·2 mm long, about 1·5 mm wide ; apex cucullate, scabrid ; border with resorption furrow. Leucocysts wide but not strongly convex, to 35 μm wide, 100–200 μm long ; dorsal surface with pseudolacunae in the basal angle (Fig. 5, D), elsewhere with large ringed or unringed pores especially towards the apical angles of some or most cells ; ventral surface eporose except for the 3–5 marginal cell rows which have numerous large pores. Chlorocysts narrow, thin-walled, in transverse section narrowly oval with oval lumen (Fig. 5, E), centrally placed and deeply enclosed on both surfaces (only exceptionally reaching either surface locally, but never distinctly exposed).

Dioecious ; male bracts resembling the branch leaves ; female bracts large, spathulate, sheathing, up to 4·5 mm long. Spores about 28 μm diameter, tetrahedral, papillose. (Not known fertile in tropical Asia, characters of fertile plants drawn


S. magellanicum
Arctic Circle
Tropic of Cancer
Equator
Tropic of Capricorn
Antarctic Circle
Meridian of Greenwich
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The London Geographical Institute.

MAP 6

from tropical American specimens.) Chromosome number 19 (Maass & Harvey, 1973, Canada).

Northern hemisphere and South America extending into the tropical zone in Central America ; East African Islands (Madagascar) ; northern India ; not known to occur in Malaysia, Australasia or continental Africa, where earlier records of the species are based on mis-determinations (Maps 6 & 9).

INDIA : Khasia, *Hooker & Thompson 1283* (BM).

TAIWAN : Tai-yuen Shan, *Inoue, Bry. Sel. Exsicc. 148* (BM).

In habit and colour closely resembling *S. perichaetiale* (with which it has on occasion been confused), *S. magellanicum* is readily distinguished by the multiporose stem cortex, the additional pores (i.e. apart from the always present triple pores) in most branch-leaf leucocysts, and the narrow chlorocysts completely enclosed by the hyaline cells. In view of its widespread distribution in the northern hemisphere and its presence both in tropical America and East African Islands, tropical records from Asia are not unexpected. However, only one such record, cited above, can be substantiated, those from Malaysia belonging properly to *S. perichaetiale*.

The list of synonyms of *S. magellanicum* is extensive. However, they are mostly based on South American types and their identity is well established ; they are therefore not included here.

Subgenus 2. ***ISOCLADUS***

SPHAGNUM subgen. ISOCLADUS (Lindb.) Braithw. in Mon. microsc. J. 14 : 48 (1875).

Isocladus Lindb. in Öfvers. K. VetenskAkad. Förh. Stockh. 19 : 133 (1862).
Sphagnum B. *Heterophylla* Lindb., tom. cit. : 134 (1862), excl. parte.
Sphagnum sect. *Heterophylla* (Lindb.) Braithw. in Mon. microsc. J. 7 : 55 (1872), excl. parte.
Sphagnum sect. *Hemitheca* Lindb. ex Braithw., Sphagnaceae Eur. & N. Amer. : 30, 85 (1880).
Sphagnum 'Haupttype' *Dentata* Warnstorf in Verh. bot. Ver. Prov. Brandenb. 22, Abhandl. : 71 (1881).
Hemitheca (Lindb. ex Braithw.) Lindb., Eur. & N. Amer. Hvitmossor (Sphagna) : 6 (1882).
Sphagnum II. *Litophloea* Russow in Schr. NaturfGes. Univ. Jurjeff 3 : 27 (1887).
Sphagnum subgen. *Litophloea* (Russow) A. LeRoy Andr. in Bryologist 14 : 73 (1911).
Sphagnum sect. *Acisphagnum* A. LeRoy Andr. in Bryologist 16 : 59 (1913).

Type : *Sphagnum macrophyllum* Brid.

Plants variable in size and colour, generally small to medium but sometimes as large as subgenus *Sphagnum*. Cortical cells of stem never fibrillose, very rarely with more than 1 pore. Branch cortex rarely uniform, normally with 1–2 perforate 'retort cells' in leaf axils differing in appearance to the, usually smaller, imperforate cortical cells. Branch leaves truncate-dentate at apex, very rarely erose-cucullate (section *Subsecunda*), never scabrid dorsally and very rarely with a resorption furrow ; never with pseudolacunae on the ventral side. Leucocysts of branch leaves nearly always fibrillose ; if efibrose, then multiporose.

Geographical range of the genus.

It is unfortunate that this, the largest and most diverse subgenus, is typified by a species which is far from being representative. Moreover, the epithets *Litophloea* and *Acisphagnum* are more familiar for this group. The application of *Isocladus* could be limited to the aberrant group of species, including *S. macrophyllum* Brid., either by avoiding the rank of subgenus throughout *Sphagnum* or by raising the sections included in it (as defined here) to equal rank. The former course, for the reasons outlined above (p. 361), was not adopted. Arguments in favour of the treatment of sections *Subsecunda*, *Acutifolia* and *Cuspidata* as subgenera are perhaps stronger but the existence of ambiguous groups whose affinities are not altogether clear creates difficulties. At present it is desirable to maintain, for example, *Squarrosa*, *Insulosa* and *Polyclada* as distinct sections, but hardly as subgenera. There would be problems in assigning these to the larger sections if the latter were raised to subgeneric status. In addition to the above-mentioned smaller sections (some of which may be regarded as occupying intermediate positions between the larger ones from a phylogenetic standpoint), there exist species which show affinities to more than one section. In Asia *S. antarense* Zant. and *S. ceylonicum* Mitt. are two examples of species which could be assigned to different sections according to the weight given to one or another character. On similar grounds, Andrews (1937) had already proposed the merging of sections *Subsecunda* and *Cuspidata*. The great majority of species of *Isocladus* can be assigned unequivocally to one of the major sections and there is nothing to be gained by following Andrews' levelling proposals.

It should be emphasized that the arrangement above is no more than provisional and will probably need considerable amendment. In particular, it is becoming increasingly obvious, superficial resemblances notwithstanding, that section *Acutifolia*, in part at least, stands close to subgenus *Sphagnum*, closer perhaps than to other groups within section *Isocladus*! (in contrast to the views of Andrews (1937), Szafran (1946) and others).

Section A. *SUBSECUNDA*

SPHAGNUM sect. SUBSECUNDA (Lindb.) W. P. Schimper, Syn. Musc. Eur., ed. 2 : 843 (1876).

Sphagnum B. *Heterophylla* c. *Subsecunda* Lindb. in Öfvers. K. VetenskAkad. Förh. Stockh. 19 : 135 (1862), excl. parte.

Sphagnum 6. *Subsecunda* (Lindb.) Schlieph. in Verh. Zool-bot. Ges. Wien 15 : 413 (1865) – Lindb., Musci Scand. : 11 (1879).

Sphagnum sect. *Hemitheca* Lindb. ex Braithw., Sphagnaceae Eur. N. Amer. : 30, 85 (1880).

Sphagnum 7. *Cyclophylla* Lesq. & James, Manual Mosses N. Amer. : 22 (1884).

Sphagnum sect. *Comatosphagnum* C. Muell. Hal. in Flora 70 : 404 (1887) – C. Muell. Hal., Gen. Musc. Frond. : 97 (1901).

Sphagnum II. *Litophloea* A. *Diplagia* a. *Acleista* 2. *Cavifolia* Russow ex C. Jensen in Festskr. Bot. Forening Kjobenhavn Halvhundredaarsfest : 72 (1890).

Type : *Sphagnum subsecundum* Nees.

Plants very variable in size and habit, usually with brownish-orange or red pigments present, sometimes almost black, seldom pale or pure green unless submerged or shaded. Cortical cells of stem in 1–3 layers, frequently with 1–2 pores. Branches usually not strongly dimorphic ; branch cortex normally with 2 distinct retort cells. Stem leaves often resembling branch leaves, at least in the upper half, sometimes considerably reduced in some boreal species. Pseudolacunae never developed. Pores of branch leaves usually small, (2·0–)3·0–6·0(–10·0) μm, and strongly ringed, often very numerous and in rows along the commissures, especially on the dorsal leaf surfaces, rarely large and unringed. Chlorocysts in transverse section oval and usually thick-walled, reaching both surfaces (rarely immersed in some African species), central or slightly displaced towards one or other face ; lumen oval except in forms modified by habitat.

Ecological range relatively wide ; mainly favouring aquatic or subaquatic habitats but including a few tropical species from terrestrial sites in montane regions of high humidity.

Geographical range of the genus. About 35 species.

This section is one of the most difficult to define yet species can usually be assigned to it without too much trouble. Forms with rows of small, thick-ringed pores in the branch leaves, stem cortex uni- or bistratose, and centrally placed, thick-walled chlorocysts may be regarded as typical. Wide departures from the archetype are, however, met with almost throughout the range of the section. Frequently only one or two of the above-mentioned characters are in evidence, not always in the same combinations. In tropical Asia efibrillose forms are known. Other species, which could possibly be separated off into subsections, are placed in section *Subsecunda* mainly on the form of their chlorocysts, coupled with relatively little leucocyst modification (i.e. leucocysts narrow, with numerous fibrils) and relatively simple stem cortex.

Section *Subsecunda* is usually considered to be the most primitive group among the Sphagna. Within subgenus *Isocladus* this may well be so, but it would be unsound to base such an assumption on purely morphological grounds, in the face of controversy regarding what features are to be interpreted as 'advanced' as opposed to 'primitive'. However, the relative lack of branch polymorphism, combined with the rarity of heterophylly, could be indicative of comparative 'primitiveness' of at least a proportion of the species of this section. Hemi-isophylly in 'advanced' sections is frequently observed in specimens from atypical habitats wherein their natural heterophylly has been suppressed. From the distributional standpoint, section *Subsecunda* is more widespread and throughout its range contains a larger number of species than section *Acutifolia* or section *Cuspidata* (section *Cuspidata* approaches section *Subsecunda* more closely than does section *Acutifolia* in this respect, and in general shows greater proximity in form to section *Subsecunda* than section *Acutifolia* does). Species intermediate in form between section *Cuspidata* and section *Acutifolia* are unknown while approaches to both of the latter sections are to be found in section *Subsecunda*. It is not unreasonable, in the face of the above evidence, to suggest that section *Subsecunda* preceded other sections of subgenus *Isocladus* during the evolution of the Sphagnales.

4. ***Sphagnum subsecundum*** Nees in Sturm, Deutschl. Fl. 2(17) : 3 (1819). (Text-fig. 6.)

S. obtusifolium Griff., Notul. Pl. Asiat. 2 : 386, t. 76 fig. 1 (1849), non *S. obtusifolium* Ehrh. (1780).

S. khasianum Mitten in J. Proc. Linn. Soc., Bot., Suppl. 1 : 156 (1859).

S. contortulum C. Muell. Hal. ex Warnstorf in Engler, Pflanzenreich 51 (= Sphagnologia Universalis) : 321 (1911), *nom. syn.*

Plants small, usually pale brown to dark rufescent, rarely pure green. Stems about 0·5–0·6 mm diameter ; central cylinder dark brown to almost black, rarely pale, yellowish ; cortical leucocysts uniformly 1-layered, usually with 1 or 2 pores.

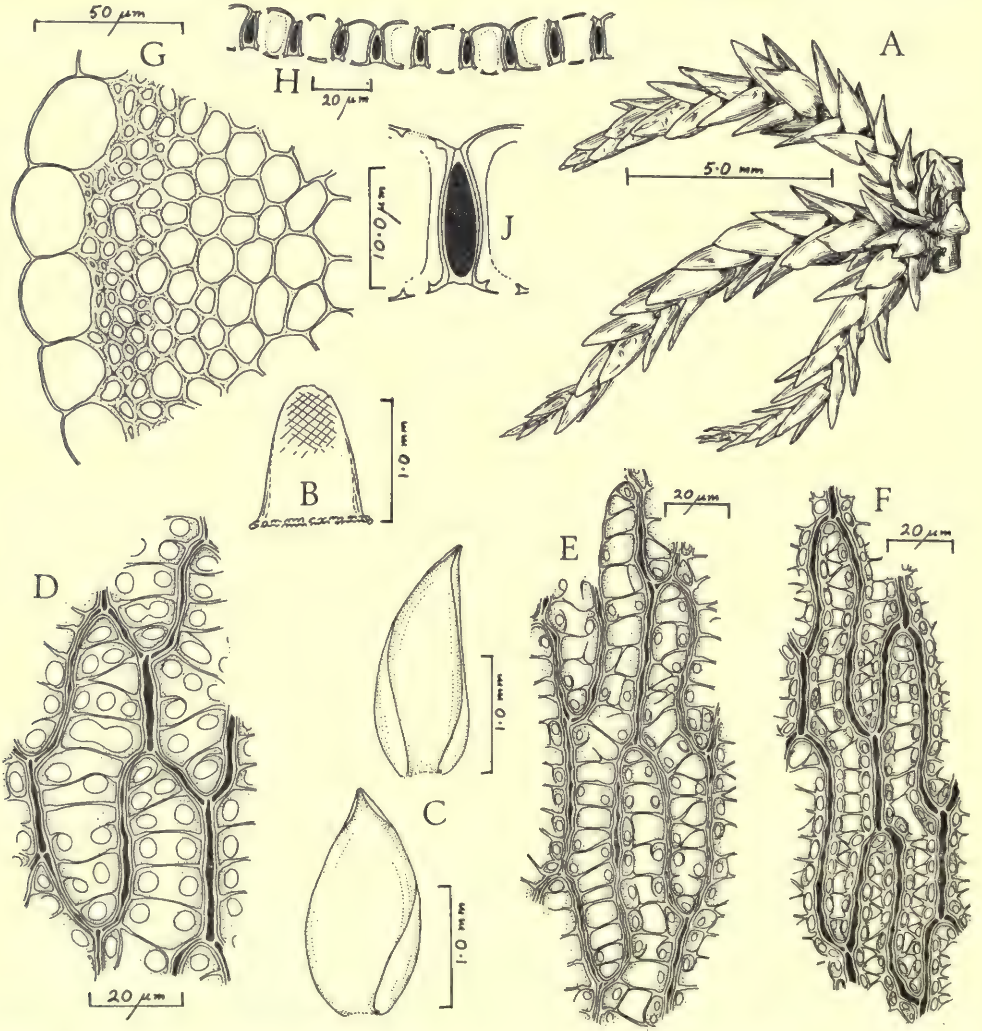
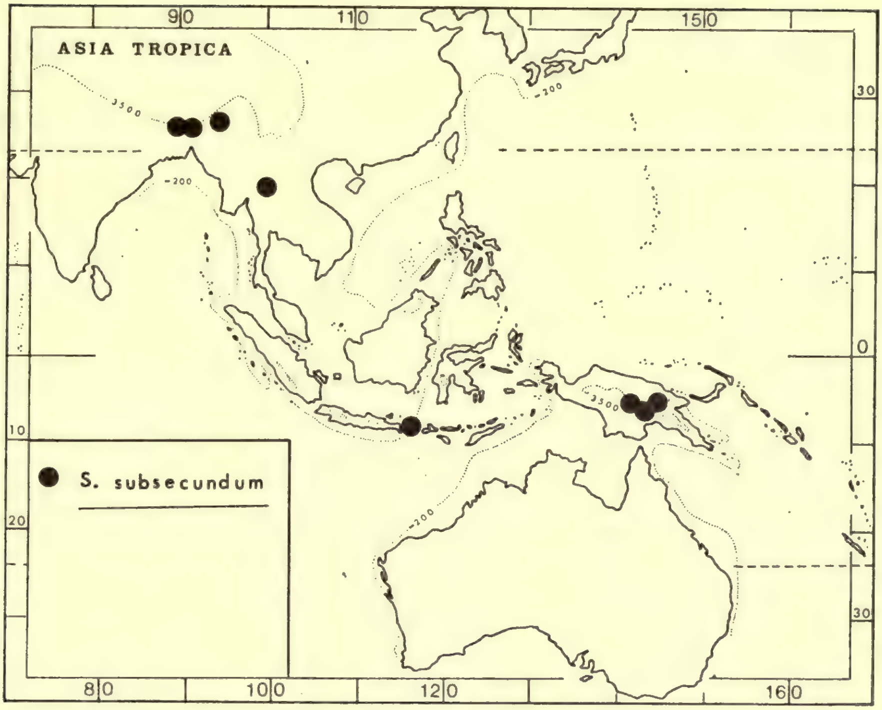


FIG. 6. *Sphagnum subsecundum* Nees : A, branch fascicle ; B, stem leaf ; C, branch leaves ; D, ventral surface of stem leaf near leaf apex ; E, ventral surface of branch leaf ; F, dorsal surface of branch leaf ; G, transverse section of stem ; H, J, transverse section of branch leaf. (All drawn from *Hooker & Thomson 1282*.)



MAP 7

Fascicles of (4–)5–6 branches up to 10·0(–13·0) mm long of which the lower 2–3 are weaker, usually unpigmented, but not otherwise dimorphic. Branch cortex with distinct retort cells. Stem leaves small, more or less triangular with rounded, eroded and usually somewhat cucullate apex, 0·8–1·1(–1·2) mm long, normally weakly fibrillose near the apex only, rarely entirely efibrose (weak stems tending towards isophylly) ; dorsal surface with few or no pores or a few leucocysts at extreme apex with small, ringed pores ; ventral surface near apex with enlarged, unringed pores (Fig. 6, D) developing here and there into larger resorption gaps, especially below. Branch leaves oval, concave, near base of stronger branches often secund and somewhat asymmetric ; 0·9–1·3(–1·5) mm long, 0·6–0·9 mm wide, apex rounded-truncate-dentate but sometimes appearing cucullate and form of apex obscured. Leucocysts narrow, 11·0–15·0 μm wide, up to 120 μm long ; dorsal surface with pores in more or less continuous series along the commissures ; pores small, *c.* 2·0–4·0 μm diam., heavily ringed (Fig. 6, F) ; ventral surface more or less eporose or with very few pores which resemble those of the dorsal surface but more or less confined to the cell angles. Chlorocysts narrow, more or less centrally placed with respect to the leaf surfaces but with slight dorsal displacement ; lumen oval in transverse section, anterior and posterior walls strongly thickened (Fig. 6, H–J). Fertile material not recorded from tropical Asia but is unlikely to differ from European material.

Eurasia from the British Isles to Japan ; North America ; Hemiarctic southwards to North East India and Thailand with outlying localities in Bali and New Guinea (Map 7).

INDIA : Khasia, *Hooker & Thompson 1282* (type collection of *S. khasianum* Mitt., BM) ; *Griffith 5* (BM). Assam : *Assam Tea Dept.* (Herb. Hampe, BM).

THAILAND : Udawn, *Hansen et al., TDBS 6435* (C).

BALI : 1857, *Zollinger* (Herb. Sande-Lacoste, L).

NEW GUINEA : Mt Sugarloaf, *Robbins 2796* (L). Mt Sarawaket, *Argent, NGBF 3/4/72 nos. 17, 18, 19, 31* (BM). Mt Giluwe, *Van Zanten 683415* (BM ; GRO).

This species is most likely to be confused with *S. ovatum* or *S. luzonense*. Forms of *S. subsecundum* as small as *S. ovatum* are always markedly heterophyllous with reduced stem leaves having few fibrils, the latter species being always isophyllous. Where isophylly occurs in *S. subsecundum*, it is confined to weak or juvenile stems occurring among more typical ones, and is rarely complete. *S. luzonense* is always more or less isophyllous, has stem leaves as large as, or larger than, branch leaves, and frequently with numerous pores on the ventral surface of branch leaves.

Close morphological similarities between some species of section *Subsecunda* have led some authors to adopt too broad a view of *S. subsecundum* (e.g. Andrews (1913), Willis (1953)), possibly, in part, as a reaction to the earlier 'over-splitting' by European sphagnologists. Due to inclusion in *S. subsecundum* of several other species from America, Australasia and elsewhere, this species has been accorded a much wider distribution than that given here. The New Guinea localities probably represent the most southern recorded stations of this species as here defined.

Anatomically, *S. subsecundum* is not a very variable species. Lax forms may be larger leaved and have more extensive fibrillation of their stem leaves, approaching in this respect *S. inundatum* Russow (= *S. subsecundum* Nees var. *inundatum* (Russow) C. Jensen in Bot. Faeroes 1 : 139 (1901)). The form of the isotype of *S. khasianum* Mitt. approaches the latter taxon. However, it is by no means established where the division, if any, between *S. subsecundum* and *S. inundatum* lies in terms of morphological characteristics. Differences in chromosome number have been indicated between *S. subsecundum* ($n = 19+2m$, Bryan, 1955) and *S. inundatum* ($n = 38+?$, Holmen, 1955), suggesting the possible derivation of the latter taxon from the former. Infraspecific polyploid series are not unknown among vascular plants and have been reported, rarely, in Musci. While recognizing the value of distinguishing phenotypically identifiable autodiploids by name, the uncertainty attached to the present taxon, particularly in the absence of cytological supporting evidence, precludes the separation of tropical Asiatic specimens into named varieties.

5. **Sphagnum ovatum** Hampe apud C. Müller in Linnaea 38 : 546 (1874). (Text-fig. 7.)

Plants small and delicate (resembling *S. subsecundum* Nees), pale orange-brown to bright orange. Stem usually dark, about 0·5–0·7 mm diameter ; cortical cells in a single layer, mostly with a single (occasionally two) pore in the outer wall. Fascicles

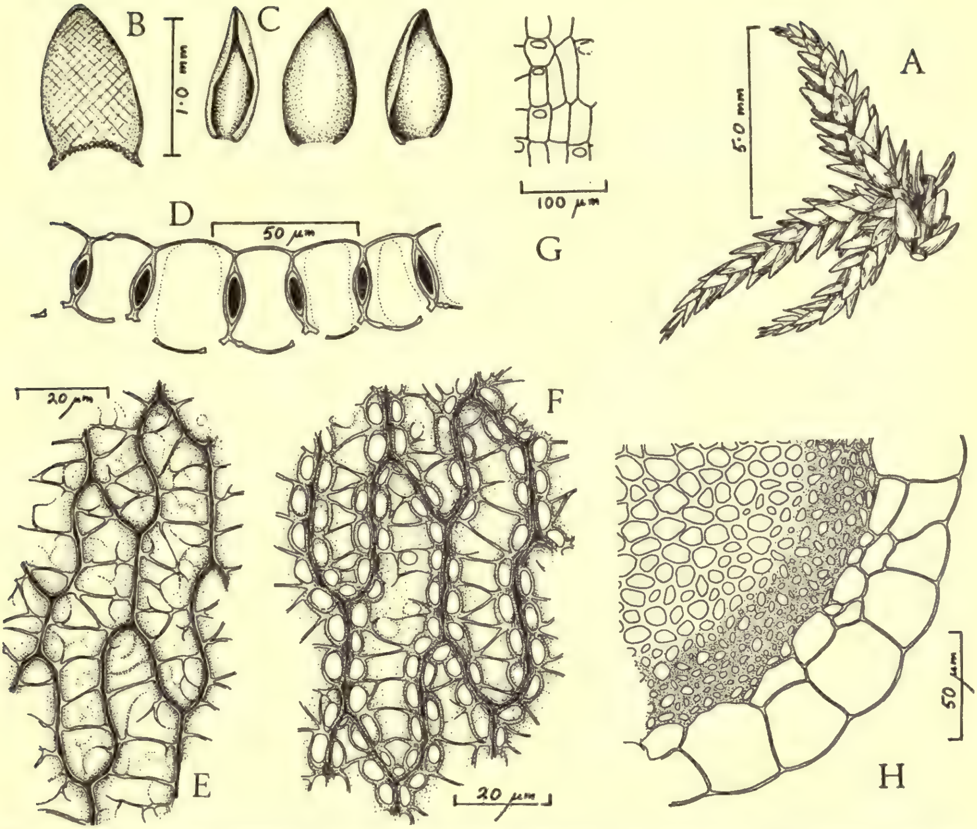
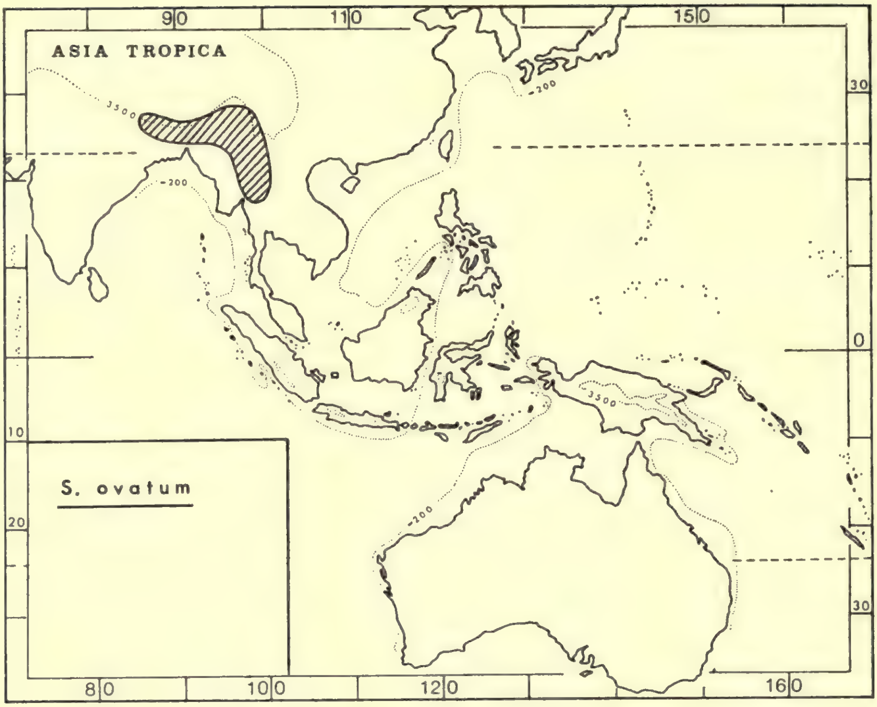


FIG. 7. *Sphagnum ovatum* Hampe : A, branch fascicle ; B, stem leaf ; C, branch leaves ; D, transverse section of branch leaf ; E, ventral surface of branch leaf ; F, dorsal surface of branch leaf ; G, stem cortex ; H, transverse section of stem. (All drawn from *Kurz 2104*.)

with (3–)5 branches which are up to 10·0 mm long, only slightly dimorphic with 1–3 weaker, less pigmented pendent ones. Stem leaves 0·9–1·2(–1·3) mm long, 0·7–1·0 mm wide, markedly concave, apex rounded and subcucullate, fibrillose and porose as in the branch leaves which they resemble but with more frequent ventral pores in some cases ; border not expanded below, evanescent towards apex. Branch leaves uniform, symmetrical and not secund, ovate and strongly concave, small, 1·1–1·3 mm long, 0·9–1·0 mm broad ; apex rounded-obtuse, erose and weakly dentate, appearing cucullate. Leucocysts in mid-leaf relatively short and wide for the section, 15–20 µm wide or more, 90–120 µm long ; dorsal surface with small, thick-ringed pores in regular rows along the commissures, near leaf apex with an occasional unringed pore in the cell mid-line ; ventral surface eporose or pores few but with several ill-defined pseudopores or reticular thickenings. Chlorocysts narrow, in transverse section with oval lumen and thick walled ; more or less centrally placed and narrowly exposed on both surfaces but distinctly less so on the ventral side. Fertile material unrecorded.



MAP 8

Asiatic continent from India to Thailand, south of the Himalaya. (Map 8.)

INDIA: Darjeeling, *Kurz 2104* (holotype, BM). Assam, *Stokoe 2* (BM). Khasia, *Griffith 302* (BM).

THAILAND: Doi Nangka, *Put 3264a* (BM). Udawn, *Touw 10615* (L); *Smitinand 11535* (L); *Hansen et al., TDBS 1030, 1031, 11521, 11529, 11545* (C; L).

This neat little species is unlikely to be confused with any other in tropical Asia except, perhaps, *S. subsecundum*. From that it is readily distinguished by the isophyllous stem leaves. The two species are closely related and one or two specimens from the Himalaya (e.g. *Norkett 8604*, Nepal) identified as *S. subsecundum* show a slight approach to *S. ovatum* in terms of stem leaf structure. Possibly *S. ovatum* represents the nearest extant derivative of the precursor of the much more widespread *S. subsecundum*.

6. ***Sphagnum luzonense*** Warnstorf in Bot. Zbl. 76 : 388 (1898). (Text-fig. 8.)

S. luzonense var. *macrophyllum* Warnstorf in Engler, Pflanzenreich 51 (= Sphagnologia Universalis) : 398 (1911).
S. luzonense var. *sordidum* Warnstorf, loc. cit.
S. densirameum H. N. Dixon in J. Siam Soc. 9 : 4 (1933).

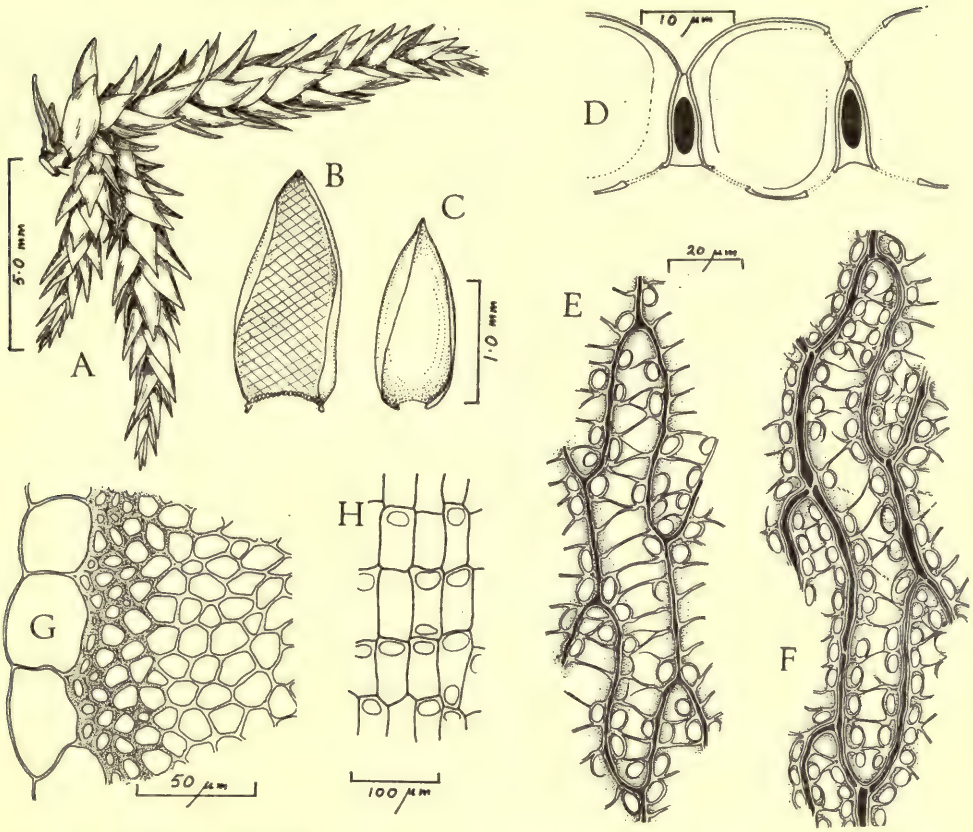


FIG. 8. *Sphagnum luzonense* Warnstorf: A, branch fascicle; B, stem leaf; C, branch leaf; D, transverse section of branch leaf; E, ventral surface of branch leaf; F, dorsal surface of branch leaf; G, transverse section of stem; H, outer surface of stem cortex. (All drawn from *Kerr 80*.)

Plants medium in size and somewhat rigid and dense in habit, becoming lax and macrophyllous in aquatic habitats, pale rufescent to dark brown, usually with underlying crimson pigmentation (strongly resembling the boreal *S. auriculatum* Schimp. in this respect). Stems about 0·8 mm diameter, internal cylinder brown to almost black, seldom pale brown; cortical leucocysts mainly in a single layer, but here and there indistinctly 2-layered, frequently with 1 or 2 large pores. Stem leaves isophyllous, as large as, or slightly longer than, branch leaves, fibrillose to base and serially porose on one or both surfaces; apex widely obtuse, rounded or subcucullate, erose and obscurely dentate; border narrow, not expanded below, evanescent above. Fascicles closely set and concealing the stem, with 2–3(–5) branches which are more or less monomorphic but 1–2 weaker and less pigmented. Branches variable in size from about 10 mm long to over 20 mm in aquatic forms. Branch leaves ovate or ovate-lanceolate, concave, narrowed above to relatively (for this section) narrow truncate, strongly dentate apex, not cucullate, rarely asymmetrical, 1·4–1·9 mm long (longer in aquatic forms). Leucocysts long and narrow, averaging 18–22 μm wide, 150–200 μm long ; dorsal face with thick-ringed small pores in interrupted or almost continuous series along the commissures, ventral surface with fewer but usually numerous pores similarly disposed or confined to the cell angles, pores often imperforate (= pseudopores, Pl. 38, E). Chlorocysts in typical states resembling those of *S. subsecundum*, in aquatic forms with thinner walls and appearing in section oval-trapezoid. Fertile specimens unknown.

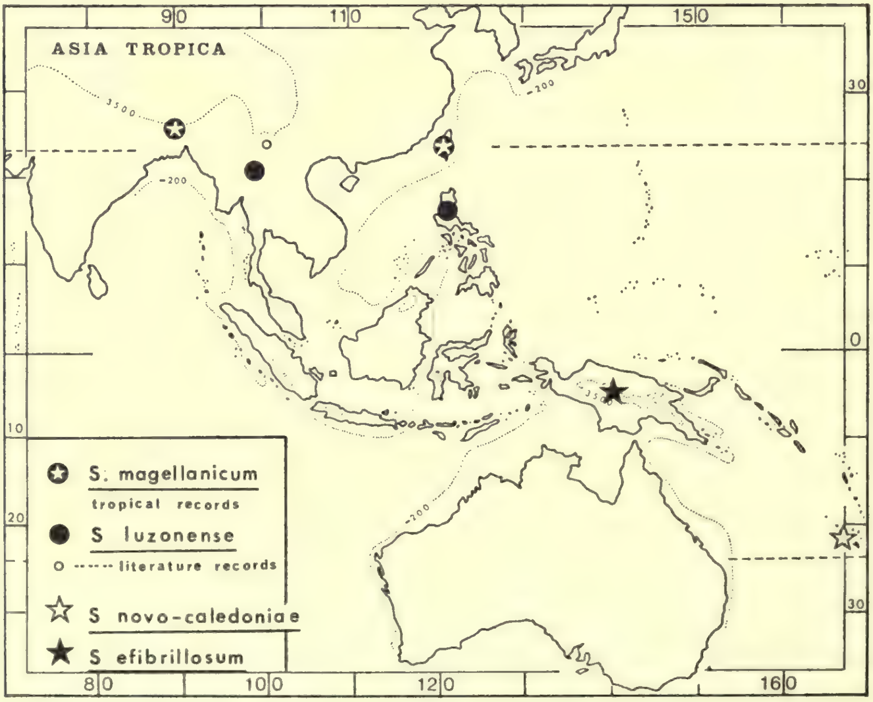
Disjunct distribution : Thailand, Vietnam and Philippines ; reported also from China (Yunnan, fid. Brotherus, 1929). (Map 9).

VIETNAM : Dalat, *van Thuy 106/C2, 107/C3, 108/C4, 112/1, 113/1* (BM).

THAILAND : Udawn, *Kerr 81* (holotype of *S. densirameum* H. N. Dixon, BM) ; *Kerr 577, 2376b* (BM). *Hansen et al., TDBS 2372, 2376b, 6411, 11522* (C, L). *Touw 10857m* (L).

PHILIPPINES : Luzon, *Loher 1047* (isotype of *S. luzonense*, BM) ; *Merrill 4911* (isotype of *S. luzonense* var. *macrophyllum*, BM).

S. luzonense may superficially resemble some states of *S. subsecundum sens. lat.* but is not difficult to distinguish from other tropical Asiatic species of section *Subsecunda*. It is a much larger plant than *S. ovatum*, with longer branch-leaf leucocysts, and is readily distinguished from *S. subsecundum* by its large, unreduced stem leaves.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✪ S. magellanicum
tropical records
● S luzonense
○ ------ literature records
☆ S novo-caledoniae
★ S efibrillosum

MAP 9

Phylogenetically, *S. luzonense* stands close to *S. auriculatum,* their common ancestry reflected by the small number of branches to a fascicle, the tendency to have very short stem internodes, the narrow, amphi-porose leucocysts and crimson pigmentation, and the facility with which *S. auriculatum* becomes isophyllous in aquatic situations. The recognition of two distinct evolutionary lines, containing, on the one hand, *S. ovatum, S. subsecundum* and their allies and, on the other, *S. luzonense* and *S. auriculatum,* is irreconcilable with the treatment by British authors of *S. auriculatum* as a variety of *S. subsecundum.* (The occasional difficulty experienced by bryologists in the separation of *S. subsecundum* var. *inundatum* from

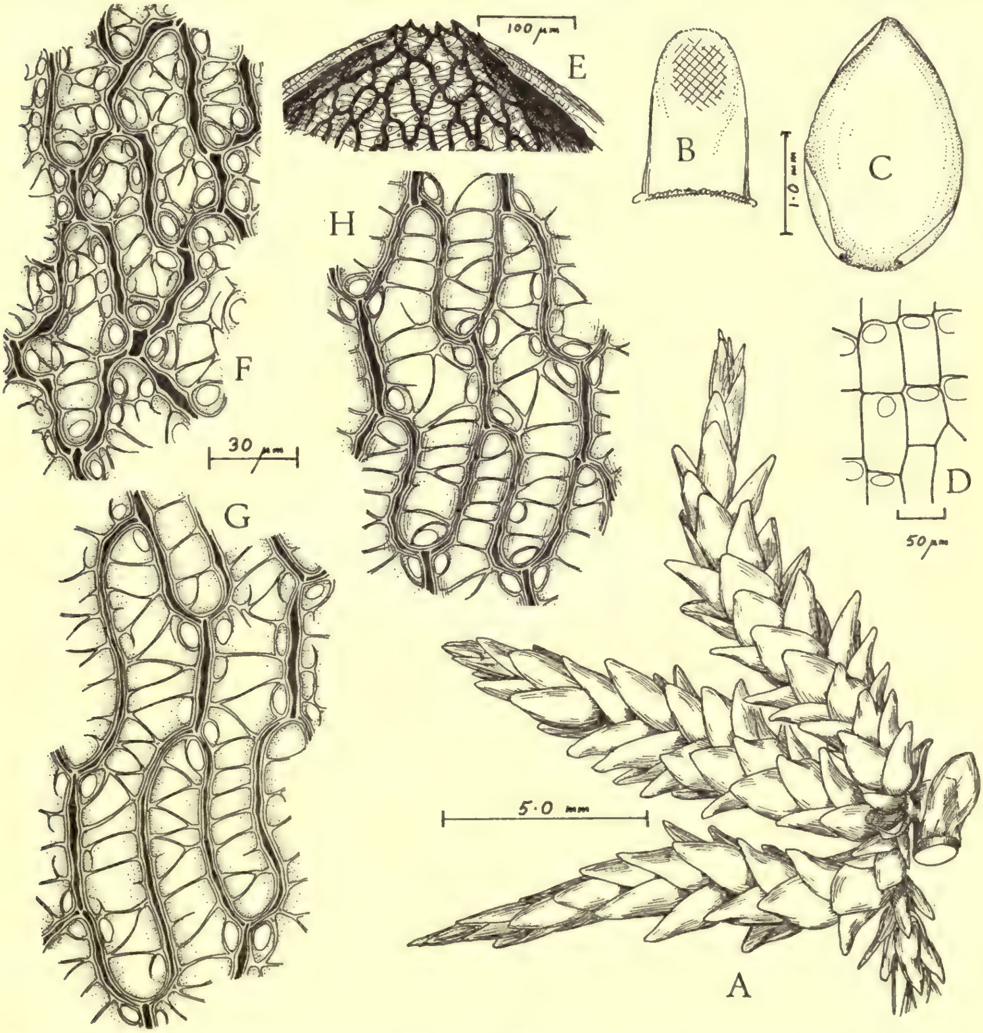


FIG. 9. *Sphagnum robinsonii* Warnstorf : A, branch fascicle ; B, stem leaf ; C, branch leaf ; D, stem cortex ; E, apex (ventral) of branch leaf ; F, dorsal surface, near apex, of branch leaf ; G, H, ventral surface of branch leaf. (All drawn from *Robinson 11006.*)

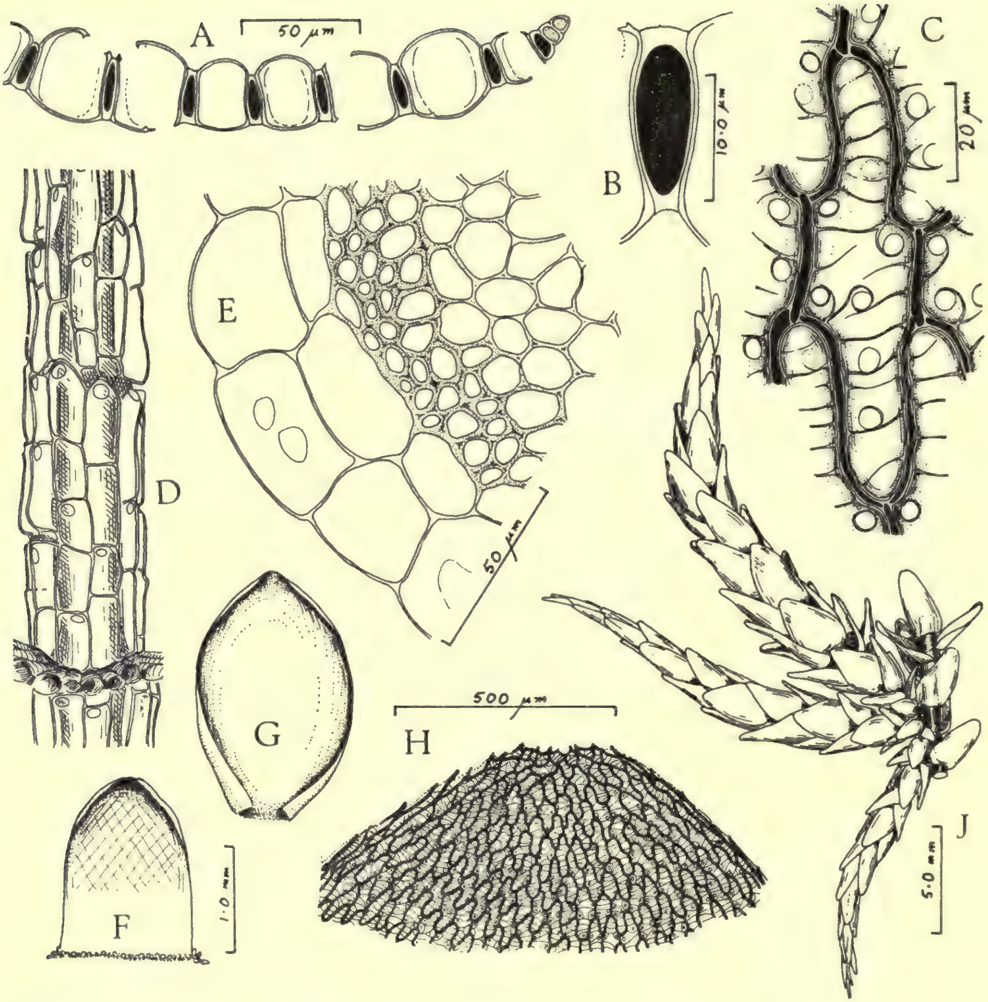


FIG. 10. *Sphagnum robinsonii* Warnstorf: A, B, transverse sections of branch leaves; C, dorsal surface of stem leaf; D, defoliated branch; E, transverse section of stem; F, stem leaf; G, branch leaf; H, apex of branch leaf (flattened); J, branch fascicle. (A–E drawn from *Robinson 11006*; F–J drawn from *TDBS 6442*.)

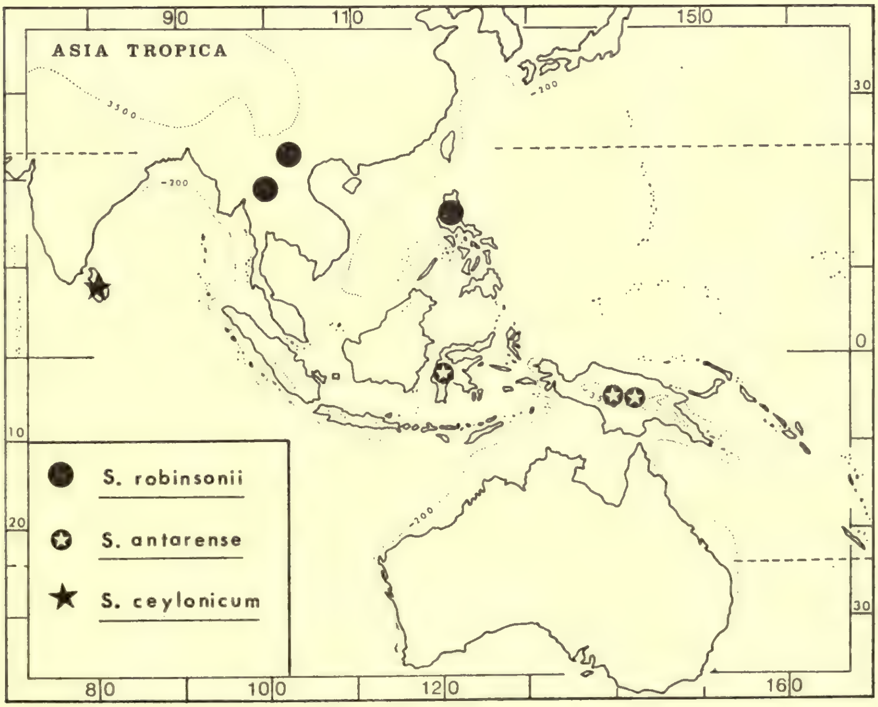
S. *auriculatum* is due partly to a misconception of the limits of the former and to apparent phenotypic convergence in response to environmental factors.)

7. ***Sphagnum robinsonii*** Warnstorf in Philipp. J. Sci., Sect. C, 7: 256 (1912). (Text-figs 9 & 10.)

S. *personatum* Hansen in Dansk bot. Ark. 20: 99, fig. 4, 8 (1961), non *S. personatum* Roiv. (1937).

S. *thailandense* Hansen, tom. cit.: 204 (1962).

Plants robust, pale brown, varying to deep orange-brown, in the type very dark below but probably humus-stained. Stems to 1·2 mm diameter; central cylinder pale to dark brown; cortical cells usually in 2 layers, in the outer layer much larger, about 50 μm wide, often with a single large pore. Fascicles of 2–4 branches, more or less dimorphic with one branch much paler and weaker, pendent branches sometimes suppressed. Stem leaves lingulate, widely rounded and erose, usually concave above and appearing almost subcucullate, very variable in size, usually smaller but occasionally larger than branch leaves, frequently hemi-isophyllous but typically fibrillose only in the upper half, anatomy of fibrillose portion resembling that of the branch leaves. Branch leaves imbricate, large, widely oval, concave, (1·6–)1·9–2·8 (–3·0) mm long, 1·7–2·0 mm wide; apex wide, dentate or frequently eroded, sometimes markedly cucullate and superficially resembling subgenus *Sphagnum*; border towards apex with partial resorption furrow. Leucocysts inflated, 20–30 μm wide, 130–150 μm long; dorsal surface with numerous thick-ringed pores in interrupted series or commonly few and confined to the cell angles and replaced, in part, by pseudopores; sometimes with a single larger resorption gap in the apical angle; ventral surface with pores more or less confined to the cell angles. Chlorocysts in section oval-rectangular, exposed on both surfaces of the leaf, more widely so on the dorsal surface, thick-walled but less so than in related species. Fertile material unknown.



MAP 10

Thailand, China and Philippine Islands (Map 10).

PHILIPPINES: Luzon, *Robinson, Bur. Sc. no. 11996* (isotype, BM).

THAILAND: Udawn, Poo Kradeng, *Hansen et al., TDBS 2367a, 6404a, 6442* (holotype of *S. thailandense*), *6450* (C).

The distribution pattern of *S. robinsonii* exactly parallels that of *S. luzonense*, both having their known strongholds in Thailand and the Philippines. Both, to some extent, resemble in this respect *S. palustre* subsp. *pseudocymbifolium*. The lack of records from other tropical Asiatic countries may represent lack of collections rather than non-occurrence. One possible explanation for the apparent disjunction assumes that, during a period of land continuity through Taiwan to the Philippines, these species were able to spread southwards and eastwards. Subsequent inundation isolated the Philippine populations from those of mainland Asia.

At first sight, *S. thailandense* appeared to be distinct from *S. robinsonii* and the disjunction in distribution certainly suggested the possibility of their being different species. Admittedly, Philippine material is rather poorly represented in the herbarium. The Danish Expedition collections, on the other hand, include a representative range of what should probably be regarded as the more typical form of the plant.

The resemblance to subgenus *Sphagnum* is only superficial, there being in *S. robinsonii* no anatomical features sufficiently distinctive to merit its separation from section *Subsecunda*. A more fitting comparison would be with *S. compactum* DC. for, among the known species of *Sphagnum*, *S. robinsonii* alone shows any approach by other taxa towards subgenus *Rigida*. The ventral pseudolacunae characteristic of subgenus *Rigida* are absent in section *Subsecunda* but most of the other features of the former are of a quantitative, rather than a qualitative nature.

8. ***Sphagnum antarense*** Wijk & Zanten apud Zanten in Nova Guinea, Bot. 16: 266, t.23 f.1 (1964). (Text-fig. 11.)

Small plants, compact, pale yellowish to light brown with faint pink undertones in the field. Stems about 0·6 mm diameter; central cylinder light brown; cortical leucocysts in 1 layer, about 30 μm wide, thin-walled or slightly incrassate and mostly with a single large pore in the outer wall. Fascicles with usually 2–3 branches, monomorphic (pendent branches suppressed ?); branches straight or slightly contorted, short, 6·0–9·0 mm long. Stem internodes short; stem leaves hemi-isophyllous, larger than branch leaves, 1·7–1·8 mm long, more or less oval-lingulate, in the upper half resembling the branch leaves. Branch leaves uniform, sometimes slightly secund, rather small, about 1·5 mm long, 0·9 mm wide; apex widely obtuse, erose sub-dentate or dentate. Leucocysts, for the section, wide, 23–30 μm or more in mid-leaf, about 120 μm long; dorsal surface without pores, or pores scarce, but with large pseudopores in some of the cell angles; ventral surface with numerous (5–7 per cell) large, 7–11 μm, pores which may be ringed or, more frequently, unringed (occasionally with additional smaller pores in the mid-line of the cell). Chlorocysts in transverse section thick-walled, with oval lumen, displaced towards, and

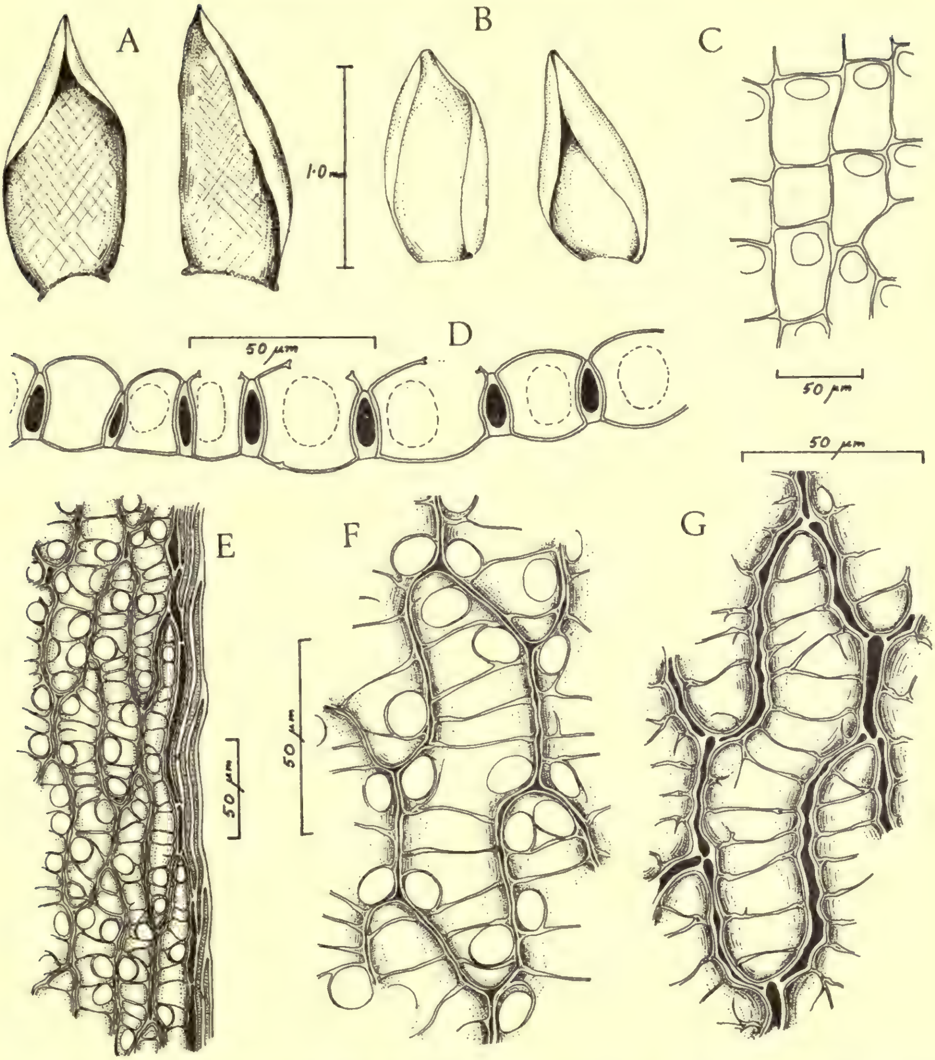


FIG. 11. *Sphagnum antarense* Wijk & Zanten : A, stem leaves ; B, branch leaves ; C, outer surface of stem cortex ; D, transverse section of branch leaf ; E, ventral surface, near margin, of branch leaf ; F, ventral surface of branch leaf ; G, dorsal surface of branch leaf. (All drawn from *Zanten 681*.)

more widely exposed on, the dorsal surface, reaching or more or less narrowly exposed on the ventral surface. Fertile material unknown.

Sulawesi (Celebes) and New Guinea in open scrub forest above 3000 m alt. (Map 10.)

SULAWESI : G. Rantemario, *Eddy 4606, 4608, 5029* (BM).

NEW GUINEA: Mt Antares, *van Zanten 681* (isotype, BM). Kubor Range, *Vink 16145, 16280b* (L); *Voss & Singigl s.n.* (L).

This curious plant seems to have no close relatives, at least in Asia. As Zanten (1964) points out, the large ventral pores, pauciporose dorsal leaf surface and dorsally displaced chlorocysts are characters normally associated with *Sphagnum* section *Cuspidata*. Within *Sphagnum* the section *Subsecunda* contains the largest number of aberrant endemic forms, many of which possibly date back to a period when the divergence between section *Subsecunda* and other sections of subgenus *Isocladus* was much narrower than it is now. It is preferable to consider *S. antarense* as a relict of this type rather than use it to support Andrews' fusion of sections *Subsecunda* and *Cuspidata*. The highly porose stem cortex and strongly thickened chlorocyst walls, together with other minor characteristics of habit, place *S. antarense* more appropriately with section *Subsecunda* than with section *Cuspidata*.

The specimens collected on Mt Rantemario in Sulawesi differ from the New Guinea plants only in the larger number of pores (of the *Subsecundum* type) on the dorsal surfaces of the leaf leucocysts.

9. ***Sphagnum ceylonicum*** Mitt. ex Warnstorf in Hedwigia 29: 195, t.4 f.7, t.7 f.14 (1890). (Text-figs 12 & 13.)

S. ceylonicum var. *robustum* Warnstorf in Engler, Pflanzenreich 51 (= Sphagnologia Universalis): 134 (1911).
S. ceylonicum var. *brachycladum* Warnstorf, loc. cit.

Plants medium-sized or rather small, pale brown or variegated with orange-brown pigments (cf. *S. subsecundum*). Stems 0·6–0·8 mm diameter; internal cylinder dark brown or, below comal area, paler; cortical leucocysts in 2–3 layers, the outermost much larger, 25–30 μm wide, thin-walled, the majority with a single large pore. Stem leaves oval-lingulate to triangular-lingulate, 1·5–1·6 mm long, 0·9–1·0 mm wide, fibrillose almost to base, above more or less identical with the branch leaves; apex obtuse, with inrolled margins; border narrow, not widened below. Fascicles with 5–6(–7) branches; branches varying in vigour but not, or only slightly, dimorphic. Branch leaves indistinctly 5-ranked, oval to oval-lanceolate, 1·5–1·8 mm long, 0·7 mm wide; apex subacute or obtuse, narrowly truncate-dentate; border very narrow, evanescent above. Leucocysts rather short and relatively wide, averaging about 25–30 μm wide, 90–110 μm long; dorsal surface very highly porose, with large, 6·0–10·0 μm diameter, ringed pores in series along the commissures and, in addition, usually with 1–4(–6) free circular ringed pores in the cell midline; ventral surface without pores but with a few incomplete pseudopores. Chlorocysts in section narrow, oval triangular with narrowly oval lumen, exposed on the ventral surface via the highly thickened, refractive anterior wall, more or less just reaching the dorsal surface. Fertile material not recorded.

Ceylon (endemic ?); reported also in Southern India (Sharma, 1949) but no specimen or other record traced (Map 10).

CEYLON: Hatton Plains, *Thwaites 262* (type collection, BM); *Fleischer, Krypt. Exsicc. II: 15*; *Alston 2499*; *Townsend s.n.* (All in BM.)

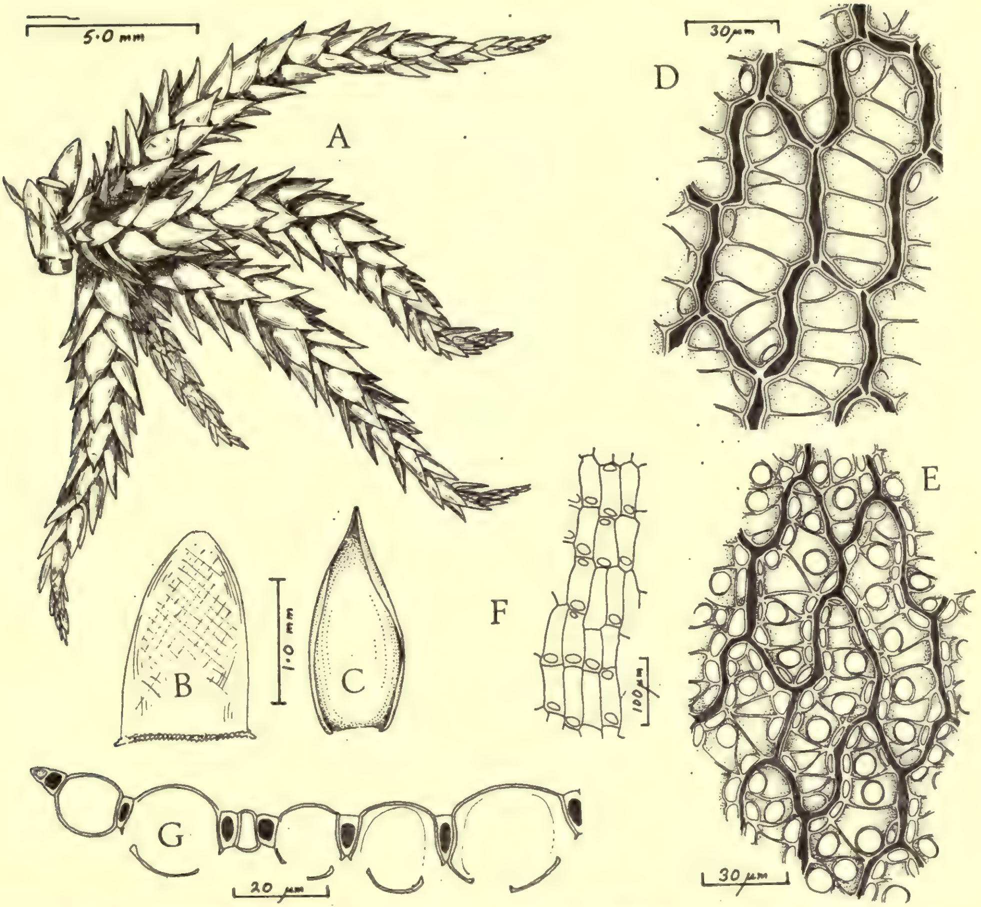


FIG. 12. *Sphagnum ceylonicum* Warnstorf: A, branch fascicle; B, stem leaf; C, branch leaf; D, ventral surface of branch leaf; E, dorsal surface of branch leaf; F, outer surface of stem cortex; G, transverse section of branch leaf. (Drawn from *Thwaites 262*.)

This is the only species of *Sphagnum* to have been discovered in Ceylon, where it is apparently more or less confined to a single area. It is not a very variable species, the varieties named by Warnstorf being trivial modifications to local environment. It is quite unlike any other Asiatic species but may well be conspecific with similar forms occurring in East Africa, Madagascar and the Mascarene Islands. The taxonomy and nomenclature of the latter group (which includes, for example, *S. beyrichianum* Warnst.) is in need of revision and it is more satisfactory to retain, for the time being, the epithet '*ceylonicum*' than to replace it prematurely with one of the earlier African names.

The large pores and ventrally displaced chlorocysts (Fig. 12, G; Pl. 38, F) persuaded some authors to include this species in section *Acutifolia*. The form of the chlorocysts in section, the general habit (consistent in cultures), the stem

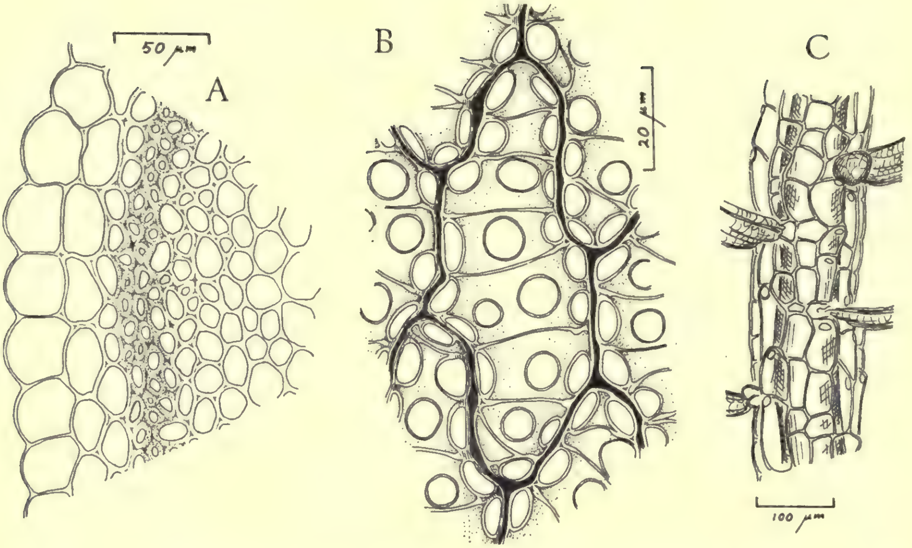


FIG. 13. *Sphagnum ceylonicum* Warnstorf : A, transverse section of stem ; B, dorsal surface of branch leaf ; C, part of branch. (Drawn from *Alston 2499*.)

structure, the serial nature of the pores and the hemi-isophyllous stem leaves are features consistent with its inclusion in section *Subsecunda*. However, the large size of the pores, the width of the leaf leucocysts and to some extent the development of the stem cortex are not *prima facie Subsecunda* characters, and may be indicative of an approach to section *Acutifolia* (but no by means sufficiently well marked to permit the inclusion of *S. ceylonicum* in the latter section). Possibly a separate subsection should be delimited to contain this and related forms.

10. ***Sphagnum novo-caledoniae*** Paris & Warnstorf apud Warnstorf in Engler, Pflanzenreich 51 (= Sphagnologia Universalis) : 297 (1911). (Text-fig. 14.)

S. novo-caledoniae Paris & Warnstorf apud Brotherus in Öfvers. finska VetenskSoc. Förh. 53A (11) : 1 (1910), *nom. nud.*

Plant small and of dense habit, ochraceous. Stem narrow, 0·3 mm diameter ; central cylinder dark brown or almost black ; cortical leucocysts in a single layer, 60–70 µm wide, apparently without pores. Fascicles with 1, occasionally 2 branches ; branches short, 4·0–5·0 mm long ; internodes very short (unbranched stems or regenerative shoots commonly interspersed with the normal ones). Stem leaves relatively large, 1·8 mm long, 0·8 mm wide, lingulate, slightly concave ; apex rounded-truncate, erose-dentate ; border narrow or evanescent ; dorsal surface of leucocysts densely porose and appearing reticulate (Fig. 14, F), pores unringed ; ventral surface with few pores confined to the cell angles, in the upper part of the leaf with considerable resorption ; fibrillae absent. Branch leaves small, up to

1·1 mm long, 0·4 mm wide ; apex rounded, erose-dentate ; border one cell wide or evanescent ; leucocysts narrow, devoid of fibrils, 8·5–11·0 μm wide, 65–90 μm long ; pores resembling those of the stem leaves in being very numerous over the whole cell surface on the dorsal side, pores unringed and sometimes irregular in outline ; ventral surface of leucocysts mostly with one or few smaller pores at the cell angles. Chlorocysts in transverse section triangular or trapezoid, displaced towards, and more widely exposed on, the ventral surface of the leaves ; walls slightly but distinctly thickened. Fertile plant unknown.

New Caledonia ; endemic. Probably aquatic or at least subaquatic. (Map 9.)

New Caledonia : Plateau de Dogny, *Le Rat* (holotype, P ; isotype, L).

This species is known only from the type collection, but its similarity to *S. efibrillosum* (below) is sufficiently well marked to establish its peculiar features as specific characters rather than freak modifications. The uniseriate cortex and narrow leaf leucocysts place this species (and the next) fairly comfortably within section *Subsecunda* in the currently accepted sense, to which Warnstorf (1911) had already assigned it.

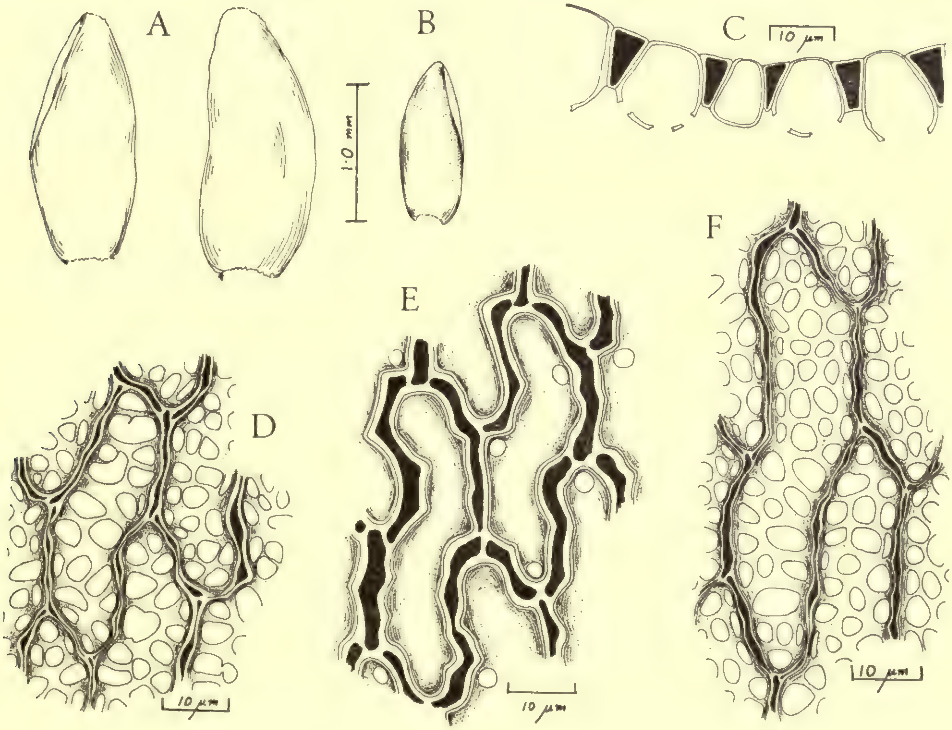


Fig. 14. *Sphagnum novo-caledoniae* Paris & Warnstorf : A, stem leaves ; B, branch leaf ; C, transverse section of branch leaf ; D, dorsal surface of branch leaf ; E, ventral surface of branch leaf ; F, dorsal surface of stem leaf. (All drawn from the type collection.)

11. ***Sphagnum efibrillosum*** A. LeRoy Andr. in Bryologist 40 : 36, figs 1–6 (1937).

A single gathering (*Brass 4473* ; Mt Albert Edward, 3680 m) of this aquatic species was made in 1933, and described by LeRoy Andrews. No similar plant from New Guinea has since been discovered nor could the holotype be located for an independent appraisal. Superficially *S. efibrillosum*, from the description and figures cited above, bears some resemblance to the North American species *S. macrophyllum* Brid. (a similarity remarked by Andrews, 1937), particularly to its variety *floridanum* Aust. The latter species is the type of Lindberg's section *Isocladus*, maintained by Isoviita, which is best regarded as a relatively recently derived section, exclusively North American and closest phylogenetically to section *Cuspidata*. The present species is provisionally placed in this work, together with *S. novo-caledoniae*, in section *Subsecunda*. Both are to be regarded as relatively ancient relict species derived from a common ancestral form and not related to the North American group ; there is no evidence to support a wider distribution, involving extreme disjunction, of the American section.

There is a marked similarity of habit and structure between *S. efibrillosum* as described and *S. novo-caledoniae*. Both have the cortical cells in a single layer, are more or less isophyllous but with larger stem leaves, bear branches mostly singly rather than in fascicles, and completely lack fibrils in the leaf leucocysts. From *S. novo-caledoniae*, *S. efibrillosum* differs in the following points : plants taller (to 130 mm), leaves of stem and branches much larger (3 times as large as in *S. novo-caledoniae*), with the apices more or less flat and strongly dentate ; leucocysts apparently with few, scattered small pores more or less confined to the cell angles.

Section B. ***CUSPIDATA***

SPHAGNUM section CUSPIDATA (Lindb.) W. P. Schimper, Syn. Musc. Eur., ed. 2 : 829 (1876).

Sphagnum B. *Heterophylla* a. *Cuspidata* Lindb. in Öfvers. K. VetenskAkad. Förh. Stock. 19 : 134 (1862).

Sphagnum 2. *Cuspidata* (Lindb.) Schlieph. in Verh. zool.-bot. Ges. Wien 15 : 413 (1865) – Lindb., Musci Scand. : 11 (1879).

Sphagnum 5. *Mollusca* Schlieph., loc. cit., *nom. nud.*

Sphagnum (*Acisphagnum*) C. Muell. Hal. in Linnaea 38 : 548 (1874), *nom. nud.*

Sphagnum 'Groupe' *Undulata* Cardot in Bull. Soc. r. Bot. Belg. 25(1) : 93 (1886).

Sphagnum sect. *Acisphagnum* C. Muell. Hal. in Flora 70 : 404 (1887) ; Gen. Musc. frond. : 97 (1901)., excl. parte.

Sphagnum D. *Laciniata* Klinggr., Leber- und Laubmoose West- und Ostpreussens : 92 (1893), *nom. nud.*

Sphagnum F. *Tenerrima* Klinggr., op. cit. : 96 (1893).

Sphagnum sect. *Mollusca* Schlieph. ex Casares-Gil in Mems R. Soc. esp. Hist. nat. 13 : 51 (1925), excl. parte.

Type : *S. cuspidatum* Ehrh. ex Hoffm.

Plants variable, small to medium, rarely approaching subgenus *Sphagnum* in size ; pale, whitish green to deep green, often yellowish or brown, very rarely (never ?)

with red pigmentation in the leaves. Stem cortex normally distinct, in two or more layers, not strongly inflated, never foraminate, often slightly incrassate and sometimes merging more or less imperceptibly with the internal cylinder. Stem leaves very variable, occasionally isophyllous, frequently hemi-isophyllous, commonly markedly heterophyllous, fimbriate or reduced. Branch leaves variable, ovate to linear, always truncate-dentate, often widely so ; border usually strong, often more than 2 cells wide. Leucocysts usually not strongly inflated ; dorsal pores normally few or absent ; ventral pores usually present in the cell angles, normally large and unringed. Chlorocysts in section triangular or trapezoid, displaced towards the dorsal surface and there always more or less widely exposed, often deeply immersed ventrally, usually rather thin-walled.

Geographical range of the genus. About 25–30 species.

Some species of this section, especially the more or less submerged forms, can be recognized in the field by their pale, flaccid habit and exceptionally narrow branch leaves. Terrestrial species usually have closely set, acute, 5-ranked branch leaves, giving the branches a prismatic appearance rarely found in other groups. Under the microscope the dorsally displaced chlorocysts, angular in section, are characteristic of section *Cuspidata*.

Phylogenetically, this section most closely approaches section *Subsecunda* (see, e.g., notes under *S. antarense*, p. 404). Certain African species, e.g. *Sphagnum truncatum* Hornsch., demonstrate a particularly close approach to the present section by the latter one. In Europe and Asia, however, the two sections are sufficiently distinct to prevent confusion.

12. ***Sphagnum cuspidatum*** Ehrh. ex Hoffmann in Deutschl. Fl. 2 : 22 (1796).

S. cuspidatum Ehrhart in Plantae cryptogamae Linn. quas in locis earum natalibus collegit et exsiccavit no. 251 (1793), *nom. nud.*

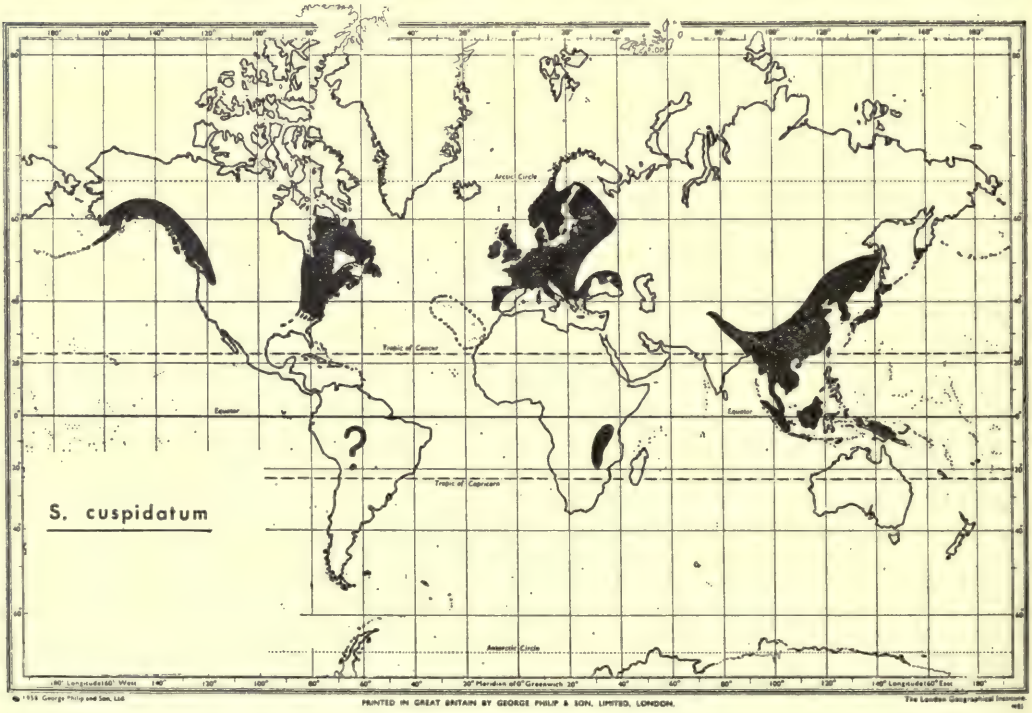
S. laxifolium C. Muell. Hal., Syn. Musc. Frond. 1 : 97 (1848).

Plants small to medium-sized, lax and flaccid or branches lax but stems rather rigid and brittle ; pale and almost colourless to deep green, antheridial branches frequently with yellow or orange secondary pigments. Stem pale green or yellowish, 0·4–0·6 mm diameter ; cortical leucocysts 30–40 μm wide, in 2–3 layers, distinct or sometimes the inner layers not sharply differentiated from the internal cylinder, walls frequently distinctly thickened, never foraminate ; internal cylinder pale yellowish. Fascicles with usually 4–5 branches ; branches long or short, weak, varying in vigour in a single fascicle but not dimorphic ; stronger branches up to 20 mm or more long but frequently much less. Stem leaves variable, triangular to triangular-lingulate, shorter than the branch leaves but always longer than wide, (1·0–)1·2–1·8(–2·0) mm long, 0·6–0·7 mm wide at base (sometimes expanded at extreme base to 1·0 mm), typically fibrillose in the upper third, and with the border very much expanded below (Fig. 15, B) but variable (see subsp. *subrecurvum* below) ; apex narrowly rounded and erose or truncate-dentate depending upon the degree of resorption ; fibrillose areas more or less resembling the branch leaf tissue but with slight to marked resorption of the dorsal surface near apex. Branch leaves five-ranked, straight or somewhat curved and slightly to distinctly subsecund, erecto-patent to patent, linear or linear-lanceolate, (2–)3–5 times as long as wide (flattened), in nature subtubular due to the inflexed or inrolled margins. Leucocysts long and narrow (11·0–)12·0–15·0(–20·0) µm wide in mid-leaf, 100–160 µm long; dorsal surface with few pores more or less confined to the cell angles, sometimes eporose, pores minute (3·0–4·0 µm); ventral surface rarely eporose, usually with 1–5 pores more or less confined to the cell angles, pores small, ringed or unringed or larger (up to 7·0 µm) and unringed. Chlorocysts in transverse section thin-walled, triangular or trapezoid, exposed on both surfaces (except sometimes in subsp. *subrecurvum*) but always more widely exposed dorsally. Female bracts sheathing convolute, oval-rectangular or oval, large, 3·5–4·0 mm long or more, 2·0 mm wide, apex rounded-obtuse, fibrillose in the upper half. Male bracts resembling the branch leaves but shorter, 1·8–2·0 mm long. Spores orange-yellow, (20–)26–32 µm diameter, papillose.

Plants aquatic or subaquatic; widespread in the north temperate zone, extending into the tropics in Malayasia (to New Guinea) and southern North America (Mexico and southern U.S.A.); East Africa; South America? (Map 11).

12a. *S. cuspidatum* subsp. *cuspidatum*. (Text-fig. 15.)

Stem leaves fibrillose in the upper half only; border usually widely expanded below with the zones of prosenchymatous cells sometimes almost confluent across



MAP 11

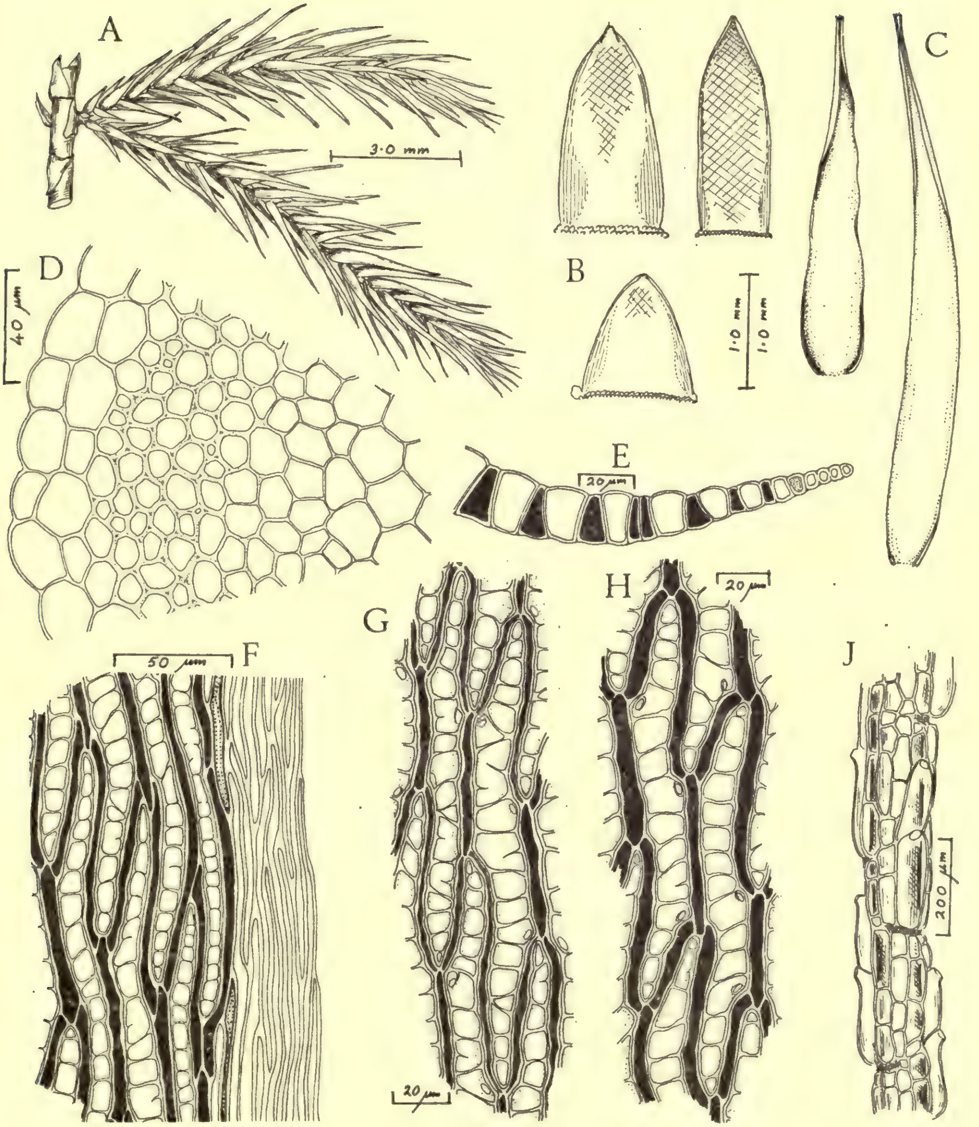
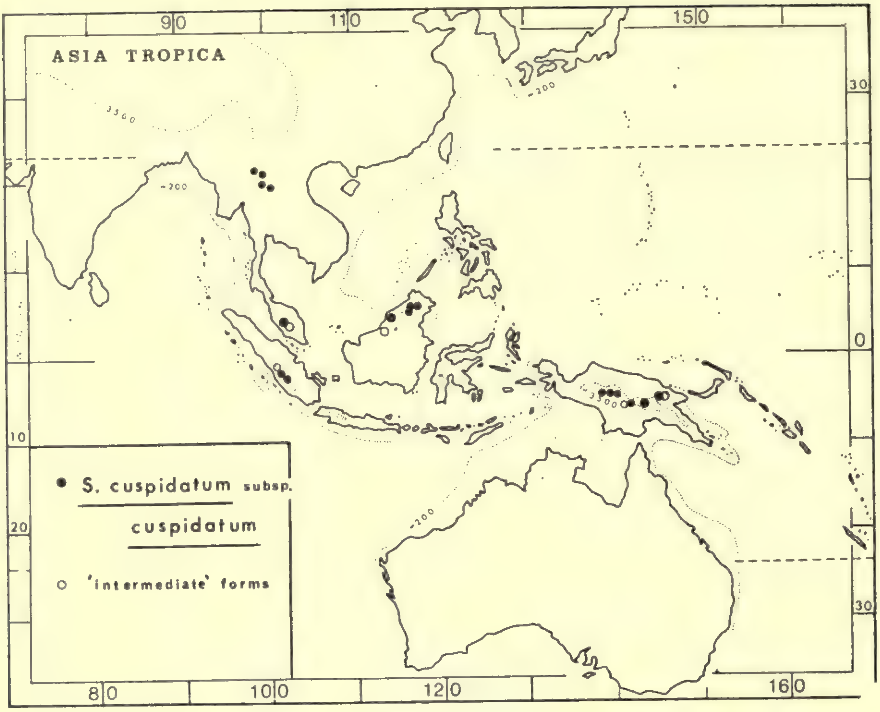

A
3·0 mm
C
D
40 µm
B
1·0 mm
1·0 mm
E
20 µm
H
20 µm
G
F
50 µm
J
200 µm
20 µm

FIG. 15. *Sphagnum cuspidatum* Ehrh. ex Hoffmann subsp. *cuspidatum* : A, branch fascicle ; B, stem leaves ; C, branch leaves ; D, transverse section of stem ; E, transverse section of branch leaf ; F, branch-leaf margin (dorsal) ; G, ventral surface of branch leaf ; H, dorsal surface of branch leaf ; J, defoliated branch. (B_2 drawn from *Kerr 250* ; B_3 from *Alston 14865*, the remainder all drawn from *Zanten 81*.)



MAP 12

the lower third of the leaf. Branch leaves, except a few at the extreme base, more or less uniform, linear and appearing subulate due to the inrolling of the margins; only 5–10 basal leaves short, very quickly grading into the normal, linear leaf form. Leucocysts of branch leaves with small (about 3–4 μm), sometimes ringed pores in the cell angles on the ventral surface. Chlorocysts always reaching the ventral surface, in section trapezoid, rarely triangular.

Pan-boreal, hemi-arctic to sub-tropical, extending into the tropical zones on high mountain ranges; widespread in Asia, recorded from most of the major island groups; in the Malay Archipelago usually confined to high mountain ridges above 3000 m alt. (Map 12).

THAILAND: Ta Samet, *Kerr 250* (BM). Pu Kio, *Kerr 585* (BM). Makam, *Kerr 107** (BM). Udawn, *Touw 11091, 11093* (L). Prachinburi, *Hansen et al., TDBS 69* (C). Khao Khio Ridge, *TDBS 11680* (C). Poo Kradeng, *TDBS 6458* (C).

MALAYA: Selangor, *Wood 1282** (BM). Pahang, *Holttum 20912, 20913* (BM).

BORNEO: Brunei, *Meijer 11511* (L). N. Borneo, *Meijer 12416* (L). Kinabalu, *Meijer 10446, 10508, 10984*, 11986* (L); also several collections in Herb. Verdoorn (BM); *Sinclair 9143* (SING). Sarawak, *Richards 5653** (BO).

SUMATRA: Tepanuli, *Alston 14865* (BM). Si Garang Garang, *Polak 154** (BO; L). G. Goh Lemboek, *Van Steenis 10171* (L).

NEW GUINEA: W. Irian, *Brass & Meyer-Drees 9758* (BO). Star Mts, *Van Zanten 17, 81* (BM; GRO). New Guinea, Eastern Highlands, Mt Wilhelm, *Eddy 3456, 3501* (BM). Wissel Lake region, *Eyma 4755** (BM; L); *Brongeroma 89* (L). Lake Habbema, *Brass 9448* (BO; L). Saruwaket Range, *Hoogland 9876** (BM); 1971, *Argent s.n.* (BM).

There is a slight but detectable tendency for specimens of *S. cuspidatum* from temperate Asiatic localities to be endowed with larger pores and wider leucocysts in their basal branch leaves than otherwise similar European material. This tendency becomes more marked in island populations and is observable in, for example, Zanten's New Guinea plants. Specimens cited above, in which this characteristic is particularly evident, and which therefore may be taxonomically closer to *S. cuspidatum* subsp. *subrecurvum* (below), are indicated by an asterisk.

In the field *S. cuspidatum sens. lat.* can always be recognized without difficulty since no other *Sphagnum* species in our area has similarly narrow branch leaves. The separation of *S. cuspidatum* subsp. *subrecurvum* (especially its variety *flaccidifolium*) from the type subspecies may, however, present difficulties and specimens which cannot be assigned unequivocally to one or other subspecies are by no means rare in collections. For further remarks on these subspecific taxa see discussion under subsp. *subrecurvum* below (p. 416).

12b. ***S. cuspidatum*** subsp. ***subrecurvum*** (Warnst.) Eddy, *comb. nov.* (Text-fig. 16.)

S. subrecurvum Warnst. in Allg. bot. Z. 1 : 134 (1895).

12b(i). ***S. cuspidatum*** subsp. ***subrecurvum*** var. ***subrecurvum.***

S. seemannii C. Muell. Hal. in J. Mus. Godeffroy 3(6) : 56 (1874).
S. javanicum Warnst. in Hedwigia 47 : 120 (1907).
S. subrecurvum var. *javanicum* (Warnst.) Warnst. in Engler, Pflanzenreich 51 (= Sphagnologia Universalis) : 263 (1911).
S. kurzeanum Hampe ex Warnst., tom. cit. : 262 (1911), *nom. syn.*
S. subrecurvum var. *borneense* H. N. Dixon in J. Linn. Soc., Bot. 50 : 69 (1935).
S. cuspidatulum C. Muell. Hal. var. *trengganuense* Anne Johnson in Gdns' Bull., Singapore 17 : 316, fig. 1f, g (1958).

Habit and colour as in *S. cuspidatum* subsp. *cuspidatum*, differing in the following anatomical details: Stem leaves variable but usually fibrillose to below the middle, sometimes almost or completely isophyllous; border strong but normally only slightly expanded below. Middle and upper branch leaves linear but usually not greatly elongated, lower branch leaves short and resembling in structure those of *S. cuspidatulum*, passing gradually or somewhat abruptly into the linear form above (Fig. 16, A–C). Ventral surface of leucocysts of lower branch leaves with large, 5–9 μm diameter unringed pores in the cell angles; distal branch leaves with smaller pores and more or less identical in anatomy to *S. cuspidatum* subsp. *cuspidatum*. Chlorocysts in section variable: in the lower leaves mostly triangular and enclosed ventrally; in the upper leaves trapezoid as in subsp. *cuspidatum*.

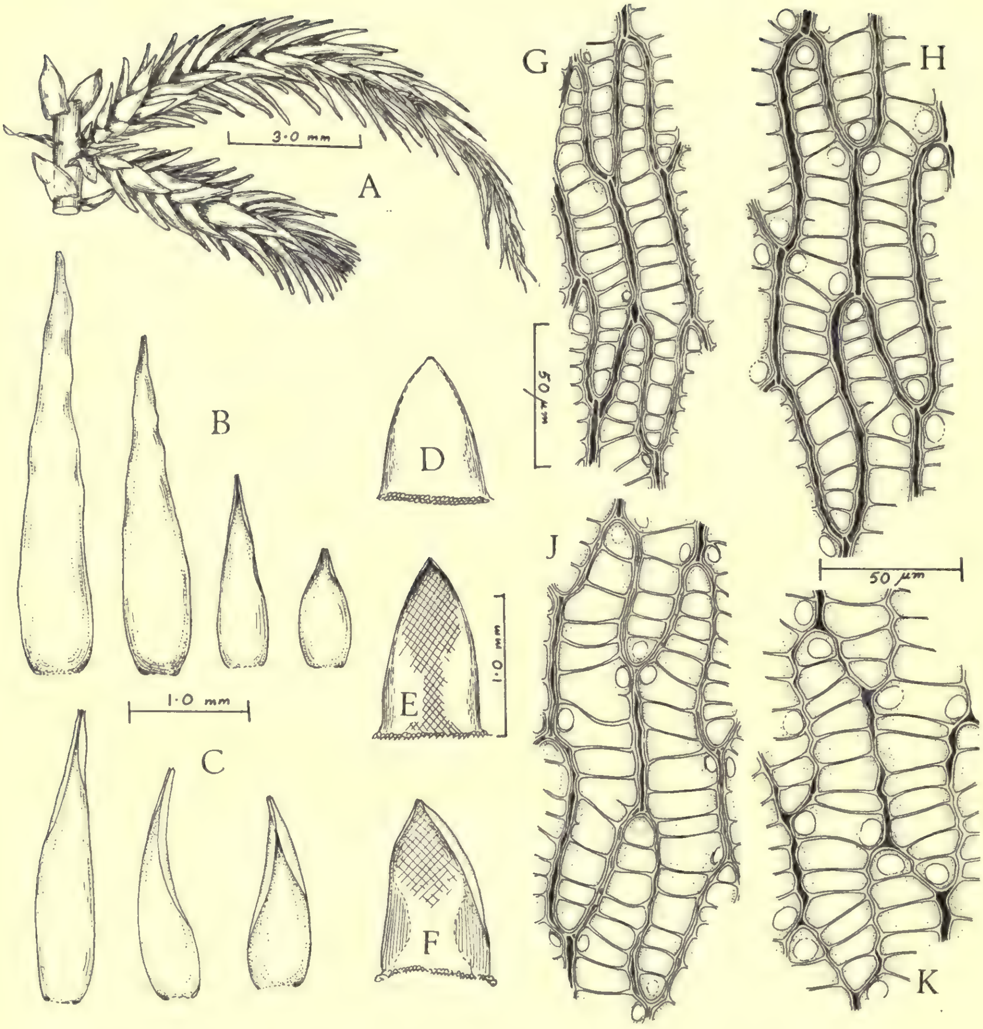


Fig. 16. *Sphagnum cuspidatum* subsp. *subrecurvum* (Warnstorf) A. Eddy: A, branch fascicle; B, C, branch leaves; D, E, F, stem leaves; G, dorsal surface of branch leaf; H, J, ventral surface of branch leaf (mid-branch); K, ventral surface of branch leaf (base of branch); (A, C, E, G, H, K drawn from *Kurz 847*; B, F, J from *Oxford Expedition 2045*; D from a specimen in Herb. Verdoorn.)

Fertile material only once seen. Apparently anisosporous with spores falling more or less into two size classes: larger spores resembling those of subsp. *cuspidatum* 25–28 µm, strongly papillose; smaller spores, 18–20 µm less papillose but otherwise similar to the larger ones. (Intermediate spores also present but fewer in number than would be expected in a continuous size gradation between the two extremes.) See Pl. 40, B–D.

Malaysia, with main occurrence in Sumatra and Java; outlying populations recorded from Thailand, New Guinea and Fiji. In similar habitats to *S. cuspidatum* subsp. *cuspidatum* but generally at lower altitudes, commonly below 2000 m (Map 13).

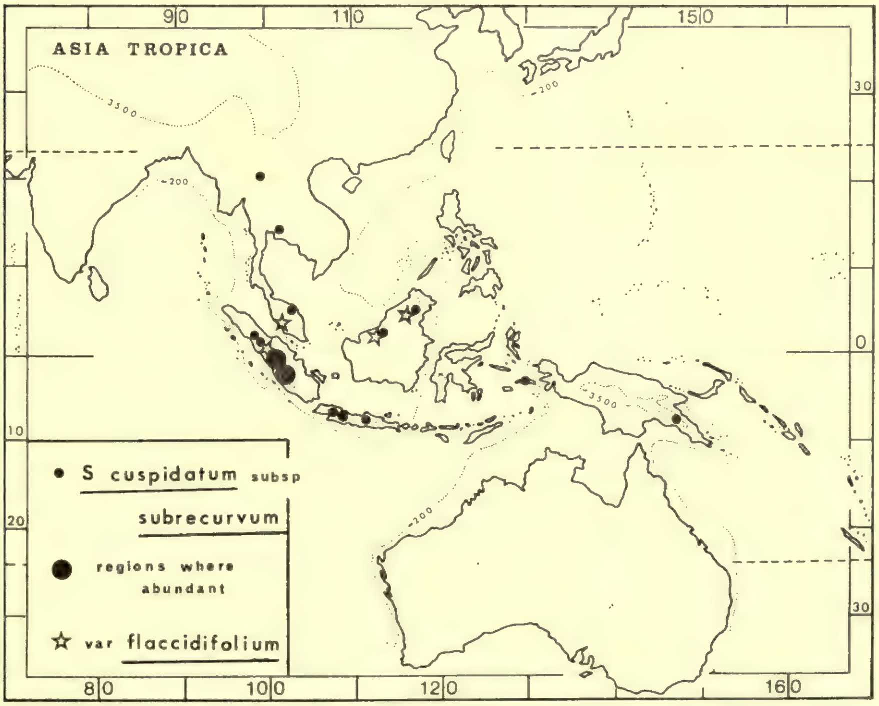
THAILAND: Phu Miang, *Smitinand 11545* (L).

MALAYA: Trengganu, *Moysey 31023* (BM; SING; type collection of *S. cuspidatulum* var. *trengganuense*).

SUMATRA: G. Koerintji, *Bunnemeijer 9602* (BM; L). Lau Deboeh, *Verdoorn 15818* (BM). Li Gelapang, *Polak 157* (BM). Central Sumatra, several collections in Herb. Verdoorn, including *Verdoorn 15819, 17559, 17571, 17572* (BM). West Sumatra, *Meijer 9545* (L). Pajakumbuh, *Meijer 6035* (L). Alahan Pandjang, *Meijer 8520* (L). Prapat, *Otto-Surbeck 58* (in fruit, L). Danau Biloeloek, *Jacobson 110* (L). Bonkoelin, *Rappard 98* (L). Tobasee Moetagindjang, *Ruttner 1038c* (L). Tongging, *Lörzing 8072* (BO; L).

JAVA: Pangrango, *Kurz 847* (isotype of *S. kurzeanum*, BM); 1969, *Eddy s.n.* (BM); *Warburg s.n.* (isotypes of *S. javanicum*, BM; BO). Preanger, *Schniffner, Iter Indicum 11397* (BM). Dieng Plateau, *Van Steenis 4495, 4545* (L). *Meijer 5836, 5837, 5838* (L). *Hochreutiner 2446, 2447* (L).

MOLUCCAS: Buru Island, *Toxopeus, BO 1668* (BO; L).


ASIA TROPICA
90
110
150
80
100
120
160
30
0
10
20
30
3500
200
● S cuspidatum subsp subrecurvum
● regions where abundant
☆ var flaccidifolium

MAP 13

Borneo: Sarawak, *Oxford Expedition (1932) 2045* (holotype of *S. subrecurvum* var. *borneense*, BM). North Borneo, *Wood 1536* (BM).

New Guinea: Owen Stanley Range, *Robbins 4248* (L).

Fiji: Taveuni, *Seemann 839* (type collection of *S. seemannii*, BM); A. C. *Smith 867* (BM).

12b(ii). ***S. cuspidatum*** subsp. ***subrecurvum*** var. ***flaccidifolium*** (Anne Johnson) A. Eddy comb. nov. (Text-fig. 17.)

S. flaccidifolium H. N. Dixon ex Anne Johnson in Gdns' Bull., Singapore 17: 316, fig. 1a, b (1959).

Flaccid, habit resembling plumose forms of subsp. *cuspidatum* and of similar dimensions or, as in the type specimen, more robust. Stem leaves triangular, less frequently triangular-lingulate, fibrillose to below the middle and with few pores; border narrow (as in var. *subrecurvum*) and not, or scarcely, expanded below. Branch leaves very long, 3·0–5·3 mm, slightly tapering to a truncate, sharply dentate apex. Leucocysts and chlorocysts as in subsp. *cuspidatum* (in the type collection) or approaching, in a few basal leaves, those of var. *subrecurvum*. Short basal leaves (of the 'cuspidatulum' type) usually few.

Malay Peninsula, Sumatra and Borneo; subaquatic, lowland (Map 13).

Malaya: Selangor, *Holttum 28317* (type collection of *S. flaccidifolium*; BM; SING); *Van Steenis 18500* (L). Pahang, *Wood 1486* (BM).

Sumatra: Pakan Baroe, *Holttum 28127* (BM). Brastagi, *Van der Wijk 1743* (L).

Borneo: Sarawak, *Richards 5653* (BM; L). North Borneo, *Meijer 12417, 12419* (L).

Although *S. cuspidatum* is a polymorphic species it has a characteristic habit and is easily recognized in the field. The pale colour combined with very narrow, often almost setaceous, leaves is not found in any other tropical Asiatic species. (*S. falcatulum* Besch., a southern hemisphere species, closely resembles *S. cuspidatum* but the range of the two species does not appear to overlap, at least in Asia.) The typical form, identical with populations from the temperate range of the species, is not common in tropical Asia, where it is confined to the higher mountain ridges. In such habitats subsp. *cuspidatum*, like *S. subsecundum*, occurs in what are probably relict populations from a more widespread Pleistocene community. *S. cuspidatum* does not appear to have penetrated very far into the southern hemisphere. The New Guinea records and some East African ones may represent the most southern occurrences of the species (the South American range needs further investigation). Other records from the southern hemisphere have proved, on examination, to belong to *S. falcatulum* or its allies.

Warnstorf's taxon *S. subrecurvum* poses many problems. In its most distinct facies there is no difficulty in separating it from typical *S. cuspidatum*, for it then resembles a chimera between the latter species and *S. cuspidatulum*. A range of forms exists which, however, connect the typical '*S. subrecurvum*' form with normal

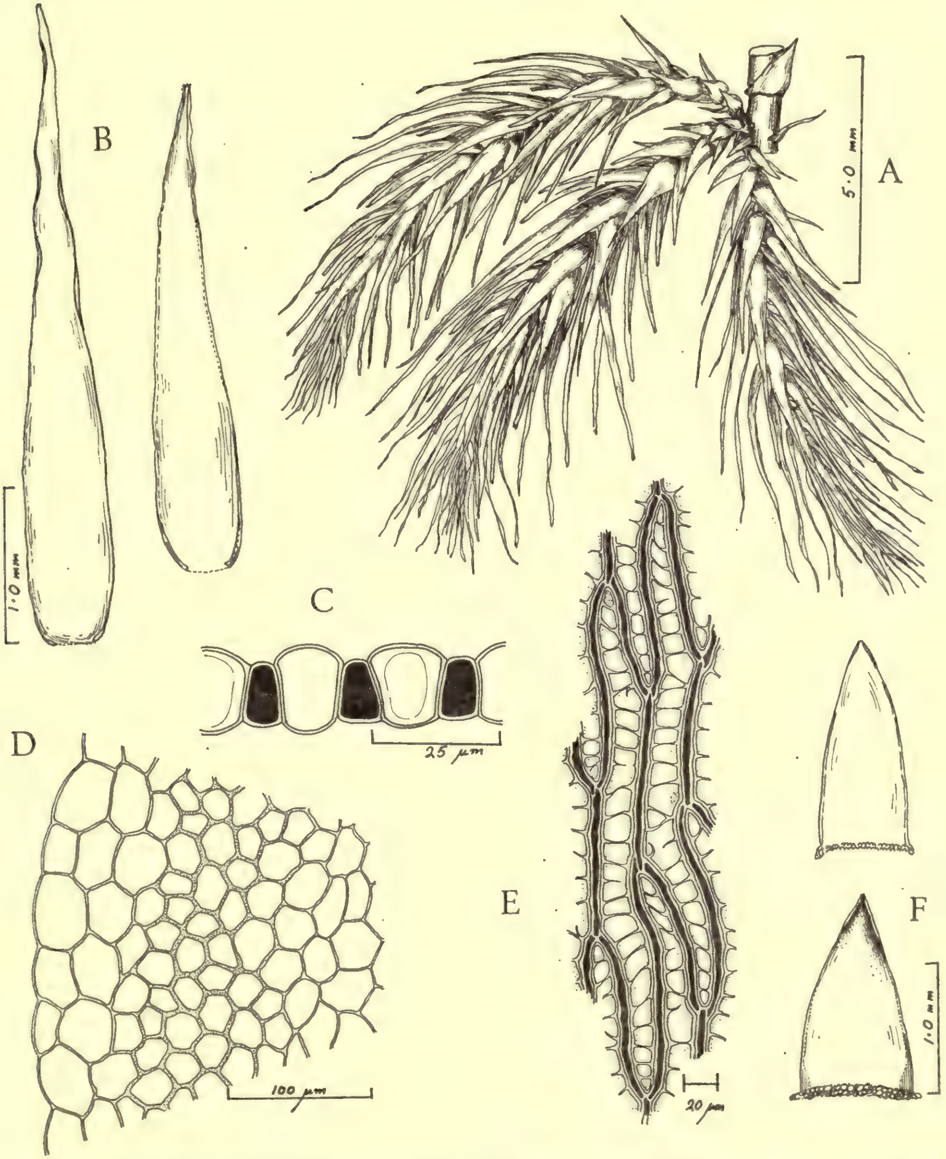

A
5·0 mm
B
1·0 mm
C
25 µm
D
100 µm
E
20 µm
F
1·0 mm

FIG. 17. *Sphagnum cuspidatum* var. *flaccidifolium* (Anne Johnson) A. Eddy: A, branch fascicle; B, branch leaves; C, transverse section of branch leaf; D, transverse section of stem; E, ventral surface of branch leaf; F, stem leaves. (Drawn from *Holttum 28317*.)

S. cuspidatum. In the past, undue emphasis has been placed on the form and structure of the variable stem leaves, the structure of which seems frequently to vary independently from the rest of the plant. Specimens with most of the leaf area fibrillose and a relatively unexpanded border have customarily been placed under *S. subrecurvum.* Intermediate plants, on that basis, have been placed arbitrarily under one or the other 'species', confusion in the herbarium reflecting the difficulties experienced by botanists attempting to name them. If due attention is paid to the more critical structure of the basal branch leaves, such difficulties will in most instances be obviated. The fact that this is not invariably true is the principal basis for reduction of *S. subrecurvum* to a subspecies of *S. cuspidatum.* The reasons for maintaining it at that rank, and not reducing it further to varietal status are twofold:

(a) The status of variety in *Sphagnum* has been so widely misused by various authors in the past that, as a taxonomic rank, the term has come to be regarded as meaningless by many modern bryologists.

(b) The derivation and limits of subsp. *subrecurvum* are by no means clear. Nevertheless, the approach to *S. cuspidatulum* demonstrable in its more extreme forms is perhaps significant. This approach is less marked than that towards *S. cuspidatum,* but the possibility of hybrid origin (i.e. *S. cuspidatum* × *S. cuspidatulum*) cannot be entirely ruled out (the occurrence of anisospory, mentioned below, lends some support to this possibility). A further possibility, that subsp. *subrecurvum* is an ancestral form from which the boreal subspecies and *S. cuspidatulum* have been derived, is also worthy of consideration. Elsewhere in tropical habitats, variation in *S. cuspidatum* does not produce forms parallel to subsp. *subrecurvum.* The latter does not therefore seem to be merely a response to a more tropical environment. Rather it is a genetically determined taxon having a preference for the lower altitude zones within the tropics.

In Sumatra and adjacent areas, *S. cuspidatum* subsp. *subrecurvum* occurs virtually to the exclusion of subsp. *cuspidatum.* Part of the difficulty encountered in the separation by bryologists of the two subspecies might be the result of introgression between native populations of subsp. *subrecurvum* and immigrant Asiatic genotypes of subsp. *cuspidatum.* (Perhaps this argument could be extended to include *S. cuspidatulum,* since that species is unaccountably rare over the main range of *S. cuspidatum* subsp. *subrecurvum.*)

S. cuspidatulum has never, to my knowledge, been found in fruit. Possibly its spores might resemble those of its close relative, *S. fallax* Klinggr., in which case they would be smaller than those of *S. cuspidatum* and less papillose. Spores from a single, well-developed capsule of *S. cuspidatum* subsp. *subrecurvum* (*Otto-Surbeck 58,* Sumatra, see above) comprised, in addition to those indistinguishable from subsp. *cuspidatum* (conclusions based on European fruiting material of the latter), smaller spores approaching those of *S. fallax* in appearance. True anisospory has not been identified in *Sphagnum* (including dioecious species of section *Cuspidata*), therefore sex differentiation probably does not account for the exceptional variation in this case. Nothing is known of the behaviour of hybrid *Sphagna,* if they occur, but a partial segregation of genomes at sporogenesis might explain the case of apparent anisospory encountered here.

A single collection of the aggregate from Trengganu is a rather odd plant. H. N. Dixon had appended the manuscript name '*S. trengganuense*' to the herbarium specimen (in BM), part of the gathering which A. Johnson (1959, *op. cit.*) described as a variety of *S. cuspidatulum*. Its stem leaves are of more or less normal '*cuspidatum*' type, but the branch leaves are those of subsp. *subrecurvum*, from which they differ in the additional, rather numerous, minute pores in the leucocysts. Such minute pores (0·5–2·0 μm) are met with, on occasion, in several members of subgenus *Isocladus*, and do not seem to have any taxonomic significance. Under the circumstances, it is best not to introduce, on the basis of a single, possibly aberrant, specimen, yet another varietal name to a list which, over the range of the species, is already excessive. Should it, in future, be distinguished at that level, it should in my opinion be placed as a variety of subsp. *subrecurvum* in the *S. cuspidatum* aggregate, rather than under *S. cuspidatulum*.

Isotype material of *S. seemannii* C. Müll. is represented in BM by a small fragment which clearly belongs to the *S. cuspidatum* complex. A later collection (*Smith 867*, BM) named *S. seemannii* exhibits characters somewhat intermediate between those of subsp. *cuspidatum* and subsp. *subrecurvum*. On balance, the latter specimen is closer to subsp. *subrecurvum* (shorter branch leaves, larger ventral pores, narrower ventral exposure of chlorocysts and stem leaf morphology) than to the type subspecies, and the occurrence of this, rather than subsp. *cuspidatum*, on Fiji is not unexpected.

The type gathering of *S. flaccidifolium* from Selangor resembles subsp. *cuspidatum* rather than subsp. *subrecurvum*, but the other specimens cited under var. *flaccidifolium* connect it, however, with the latter, of which it seems to be an ecological form. It therefore seems appropriate to give it no more than varietal status. All specimens are from exceptionally low-lying localities.

13. ***Sphagnum cuspidatulum*** C. Muell. Hal. in Linnaea 38 : 549 (1874). (Text-fig. 18.)

S. rufulum C. Muell. Hal., tom. cit. : 548 (1874) (fide. Warnst. in Engler, Pflanzenreich 51 (= Sphagnologia Universalis) : 186 (1911)).
S. feae C. Muell. Hal. in Nuov. G. bot. ital. 23 : 601 (1891), *nom. nud.*
S. malaccense Warnst. in Hedwigia 31 : 175 (1892).
S. acutum Warnst. in Allg. bot. Z. 1 : 136 (1895) ; in Engler, Pflanzenreich 51 (= Sphagnologia Universalis) : 191 (1911), excl. var. *hakusanense* Warnst.
S. cuspidatulum var. *malaccense* (Warnst.) Warnst. in Engler, Pflanzenreich 51 (= Sphagnologia Universalis) : 187 (1911).
S. cuspidatulum var. *fibrosum* Warnst., loc. cit.
S. cuspidatulum var. *fuscescens* Warnst., tom. cit. : 188 (1911).

Plants usually fairly robust and pale, green or yellowish, but varying to small, dense and brown. Stems up to 0·8 mm diameter, internal cylinder pale yellowish to light brown ; cortical leucocysts mostly in two layers, 20–25 μm wide, their walls nearly always distinctly, sometimes strongly, thickened, never foraminate. Fascicles usually of 4(–5) branches which are more or less dimorphic ; two spreading branches (4·0–)6·0–12·0(–15·0) mm long, 2 (frequently 3) pendent branches up to

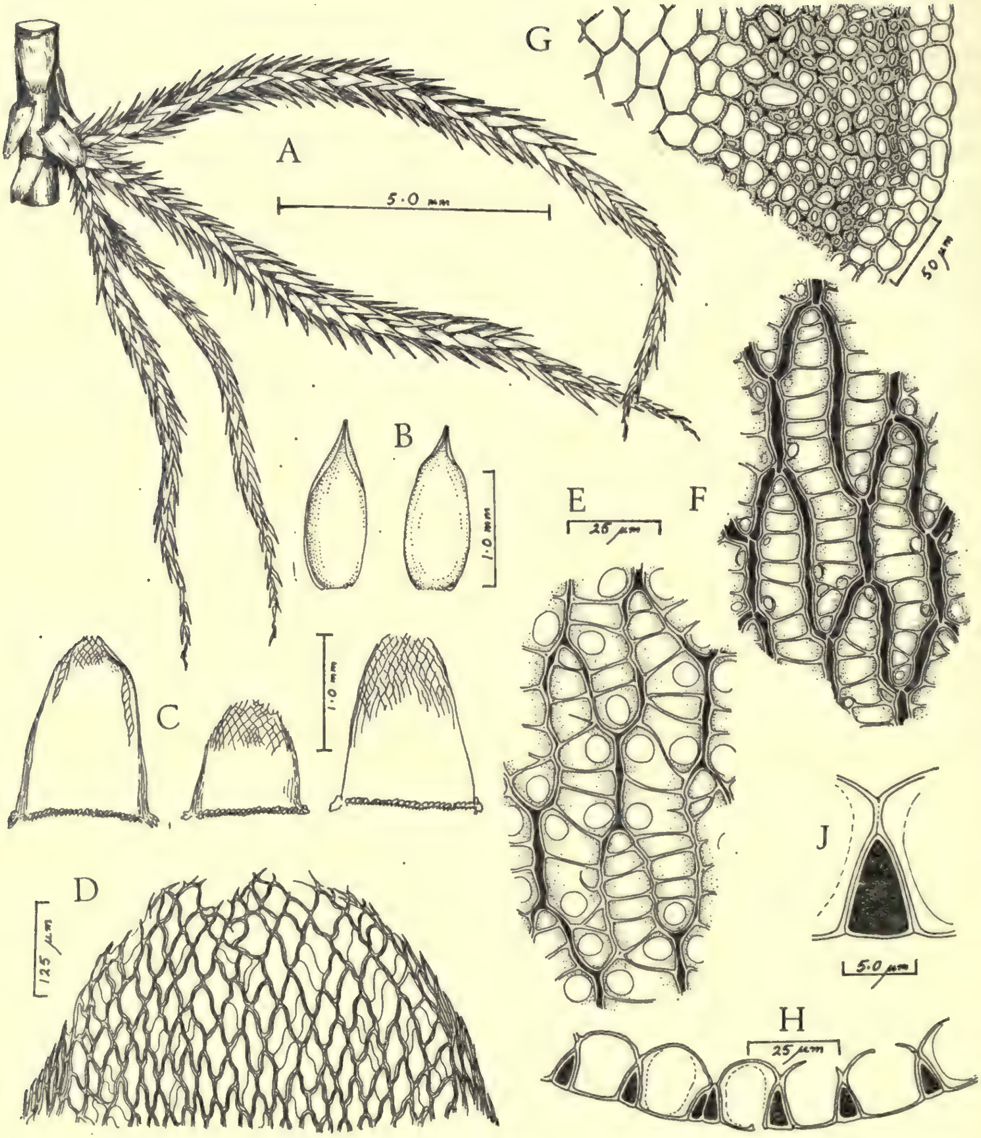
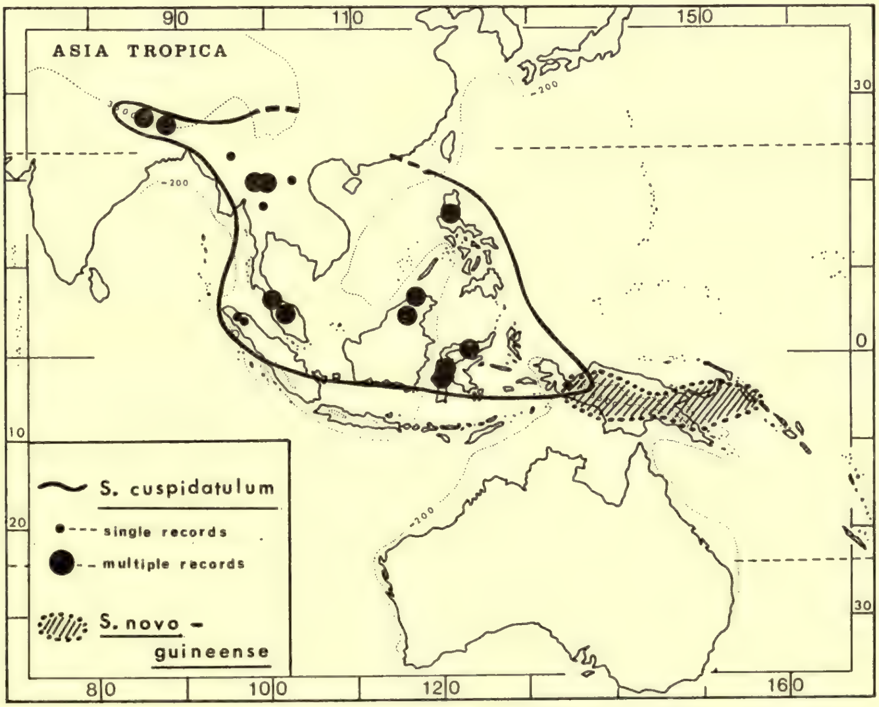

G
A
5·0 mm
50 µm
B
1·0 mm
E
25 µm
F
C
1·0 mm
J
D
125 µm
5·0 µm
H
25 µm

FIG. 18. *Sphagnum cuspidatulum* C. Muell. Hal. : A, branch fascicle ; B, branch leaves ; C, stem leaves ; D, apical part of stem leaf ; E, ventral surface of branch leaf ; F, dorsal surface of branch leaf ; G, transverse section of stem ; H, J, transverse section of branch leaf. (Stem leaves selected from various Malaysian specimens, the remainder drawn from *Holttum 14881*.)

10·0 mm. Stem leaves rather variable in size but more or less constant in anatomy, small and almost square or elongate and rectangular, (1·0–)1·3–1·5(–1·6) mm long, 0·8–1·2 mm wide, normally efibrose throughout but frequently with a small zone near apex with protuberances on the internal commissural walls of the leucocysts (basal rudiments of fibrils), very rarely with complete fibrils in one or two cells; apex widely truncate and more or less fimbriate across the whole apical margin (extending, at times, a short distance down the lateral margins), rarely somewhat tapered to a narrower apex but always fimbriate across the extreme tip; border strong below, evanescent above, usually only slightly expanded below, very rarely greatly widened in extreme forms (e.g. the type collection of S. *acutum*). Branch leaves lanceolate to oval-lanceolate, always pentastichous, uniform, (1·0–)1·3–1·5(–1·6) mm long, 0·5–0·9 mm wide; upper margins inrolled or inflexed; apex narrowly truncate-dentate; margin 2–3 cells wide, without resorption furrow. Leucocysts about 20 μm wide, 100–160 μm long; ventral surface porose, with large, circular unringed pores mostly adjacent to the cell angles, pores 7·0–8·0 μm diameter; dorsal surface without pores or with a single resorption gap in or near the apical angle, elsewhere with rather small pseudopores in some of the lateral angles which rarely become perforated. Chlorocysts in transverse section triangular, thin-walled, widely exposed on the dorsal surface, enclosed on, or here and there just reaching, the ventral surface. Dioecious ? (fruiting plants unknown); male plants usually small, fuscous.



Map 14

From Northern India and Nepal to Java and Sulawesi with a single record from New Guinea ; north to southern China and possibly southern Japan. A widespread and locally abundant species of open montane forests throughout tropical oceanic regions of Asia, but remarkably rare in Sumatra and absent from Java (Map 14).

NEPAL : Takshinder, *Noordijk s.n.* (several gatherings, L).

INDIA : Khasia, *Hooker & Thomson 1284* (type collection of *S. cuspidatulum*, BM). Sikkim, *Hooker & Thomson 1290, 1291* (syntype collections of *S. rufulum*, BM), *1286, 1294, 1296* (BM). Darjeeling, *Ribu 20* (BM). *Rhomoo 72b* (type collection of *S. cuspidatulum* var. *fibrosum*, BM). *Kurz 2109, 2291* (BM). *Lal Dhaj 83* (BM).

BURMA : Bhanco, 1886, *Fea s.n.* (type collection of *S. feae*, BM).

THAILAND : Doi Angka, *Kerr 29* (BM) ; *Garrett 322* (BM) ; *Hosseus 349a* (BM). Chiengmai, *Robbins 3642, 3643, 3644* (L). Phu Miang, *Hansen et al., TDBS 11525, 11554* (CO ; L). Khao Khio, *Smitinand & Sleumer 8325, 8326, 8328* (L) ; *Larsen, Smitinand & Warncke 71* (L). Payap, *Touw 9792, 9793, 9794, 9795* (BM ; L). Udawn, *Touw 10687* (BM ; L).

LAOS : Pu Bia, *Kerr 475, 518, s.n.* (BM). Pu Muten, *Kerr 487* (L).

MALAYA : Kedah, *Holttum 14881* (BM ; SING). Perak, *Sheffield 23* (BM) ; *Wray 902* (type collection of *S. malaccense*, SING). Pahang, *Henderson 11781, 17877b* (BM) ; *Spare 3544* (BM) ; *Holttum 23301, 23530* (SING) ; *Ridley 1026* (BM).

SUMATRA : Gajolenden, *Van Steenis 10113, 10166* (L).

PHILIPPINES : Luzon, *Robbins 4049* (L) ; *Curran, Merritt & Zschokke 16395* (BM).

SULAWESI : Menado, *Possomeer s.n.* (BO) ; *Steup 13, 1099* (L) ; *Eyma 3661* (L). Momboeling, *De Froideville 159* (BO), *144a* (L) ; *Everett 670* (BM) ; *Warburg s.n.* (L). Enrekang, *De Jong 108* (BO) ; *Van Steenis 13* (L). G. Rantemario, Pokapindjang, *Eddy 4506, 4514, 4736, 4830* (BM) ; *Eyma 25463* (BM ; L).

BORNEO : Kinabalu, *Gibbs 4145* (BM) ; *Meijer 11955, 11959, 11750, 12492, 12694* (L). Crocker Range, *Meijer 12144, 12166, 12432* (L). Kamborangah, *Holttum 25463* (BM).

NEW GUINEA : West Irian, Arfak Mts., *Gibbs 6006* (BM).

Sphagnum cuspidatulum is quite distinct from all other species of the group in tropical Asia with the exception of *S. novo-guineense* (see notes under that species, below). The form and position of the chlorocysts combined with the absence of fibrils in the strongly fimbriate stem leaves are not found in other Indo-Malayan species and are more reminiscent of such Eurasian taxa as *S. lindbergii* Schimp., or the American *S. pulchricoma* C. Muell. Hal. In nature *S. cuspidatulum* varies in size according to degree of exposure and periods of relative dryness. The first described specimens were not average plants, being smaller and having, in some cases, darker pigmentation. Subsequently the more usual form, following Warnstorf, has been unjustifiably distinguished by the varietal name '*malaccense*'.

As far as records indicate, in spite of the abundance of the species, and the large number of collections made of it, it has never been found in fruit. On the other hand, male plants seem to be not infrequent. These tend to be smaller, with the antheridial branches somewhat darker in colour, and in general conform to the 'var. *cuspidatulum*'. Clones which covered large areas of forest floor in the Latimojong Mountains of South Sulawesi showed many intergradations between '*cuspidatulum*' and '*malaccense*' extremes. Warnstorf's S. *acutum* from Borneo seems to be simply a form with exceptionally expanded border in the stem leaves, no doubt representing a local genotype but probably not worthy of varietal or subspecific distinction.

Attention may be drawn to the coincidence of the apparent rarity of this species in Sumatra and Java, with the relative frequency there of S. *cuspidatum* subsp. *subrecurvum* (see notes under that taxon, above). This phenomenon cannot be explained in terms of ecology since suitable habitats abound in both countries. The gap in an otherwise fairly continuous distribution in Malaysia and tropical continental Asia seems to be explicable only in terms of introgression between this species and S. *cuspidatum sens. lat.* The above-mentioned degree of anisospory seen in a specimen of the latter (see p. 418) may lend support to such an hypothesis.

14. ***Sphagnum novo-guineense*** Fleischer & Warnstorf apud Warnstorf in Engler, Pflanzenreich 51 (= Sphagnologia Universalis) : 520 (1911). (Text-fig. 19.)

Very similar in habit to robust forms of S. *cuspidatulum* but always pale, never fuscous. Stem 0·6–1·2(–1·5) mm diameter ; internal cylinder yellowish ; cortical cells usually incrassate, sometimes more or less thin-walled, 20–30 μm wide, in 2–3 layers, never foraminate, frequently grading internally with the woody cylinder. Fascicles with 4–5 branches which are not sharply dimorphic ; 2 spreading branches up to 25 mm long. Stem leaves 1·3–1·6 mm long, up to 1·0 mm wide at the base, very variable in outline and areolation, typically rectangular-lingulate or trapezoid and gradually narrowed to a widely truncate-fimbriate apex (which, however, is rarely as wide as in S. *cuspidatulum*), at the other extreme with apex rounded obtuse with only a minute portion at the extremity fimbriate ; fibrillose at least in the upper third (and usually a few cells at leaf base) even in strongly fimbriate leaves, and almost to the base in extreme forms ; border distinct in mid-leaf, slightly widened or indistinct below, evanescent above. Branch leaves pentastichous, broadly lanceolate, resembling S. *cuspidatulum* but somewhat larger on average, 1·4–1·8 mm long, 0·7–0·9 mm wide. Leucocysts slightly wider and shorter than in S. *cuspidatulum*, but not measurably so ; ventral surface porose with rather small, circular, unringed pores, 4·0–6·0 μm, in the cell angles but somewhat distant from the commissures (by about 2·0 μm) ; dorsal surface without pores but with frequent pseudopores, the latter occasionally in series of two or three along the lateral commissures. Chlorocysts in transverse section triangular, thin-walled, exposed dorsally but deeply enclosed ventrally, not reaching much beyond half way to the ventral leaf surface. Fertile material unknown.

Endemic to New Guinea and Bougainville (Map 14).

NEW GUINEA : Arfak Mts, *Pulle 832* (BM). Mt Goliath, *De Kock 16* (isotype, BO). Mt Antares, *van Zanten 444a, 446* (BM ; GRO). Sibil Valley, *De Wilde 829* (BM).

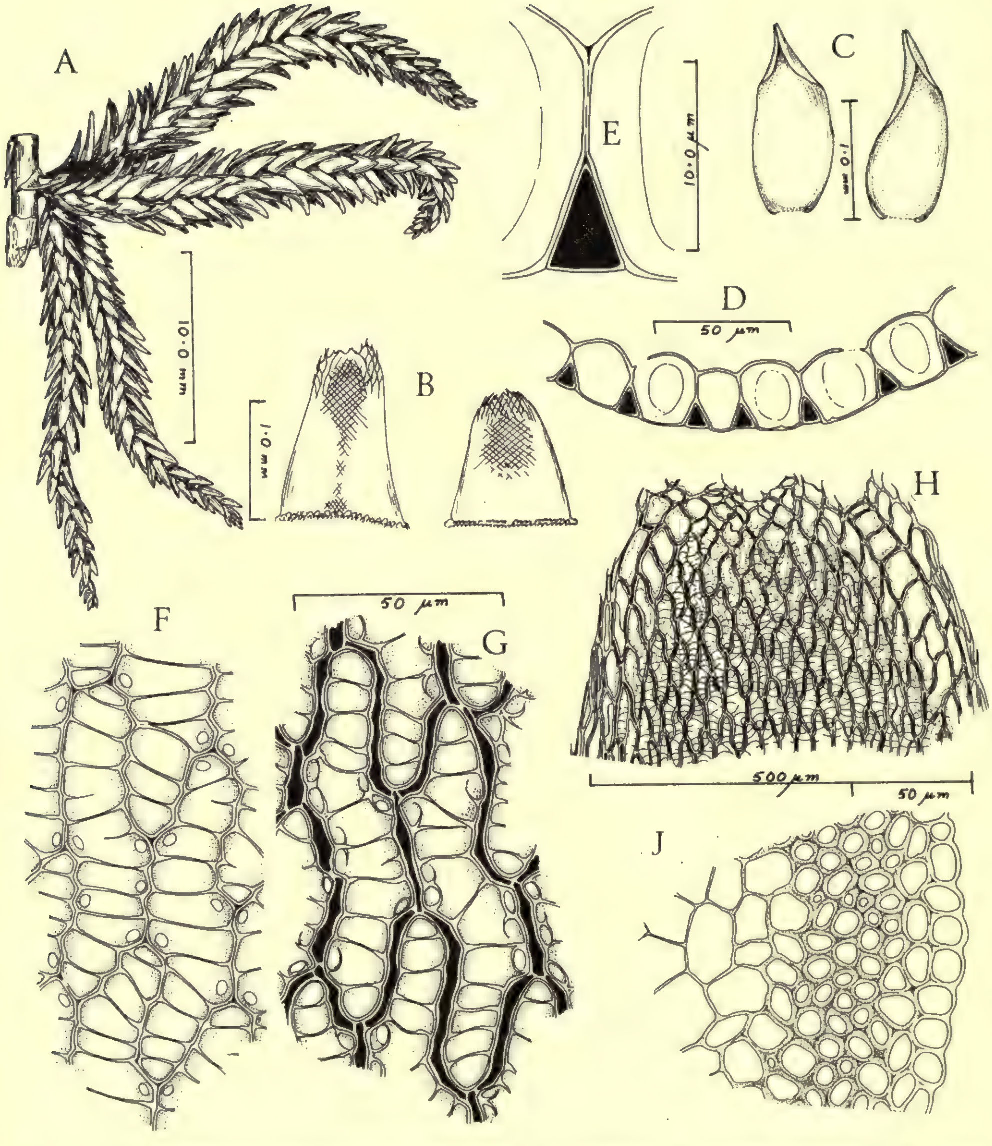

A
10·0 mm
E
10·0 µm
C
1·0 mm
D
50 µm
B
1·0 mm
H
500 µm
50 µm
F
50 µm
G
J

FIG. 19. *Sphagnum novo-guineense* Fleischer & Warnstorf: A, branch fascicle; B, stem leaves; C, branch leaves; D, E, transverse section of branch leaf; F, ventral surface of branch leaf; G, dorsal surface of branch leaf; H, apical part of stem leaf; J, transverse section of stem. (All drawn from *Pulle 832*.)

W. Irian, Nettori Range, *Van Royen & Sleumer 7464b* (L). Wissel Lakes, *Vink & Schram 8747* (L). Mt Hellwig, leg. ? (det. Fleischer no. 832 ; L). Bougainville, *Schodde & Craven 3918* (BM).

S. novo-guineense is related to, and most closely resembles, *S. cuspidatulum*. It is readily distinguished from the latter by its always fibrillose stem leaves, and relatively small branch-leaf pores. The branch leaves, although similar to those of *S. cuspidatulum*, are slightly more concave towards their apices, causing the branches to have a less prismatic appearance than the sharply angled ones of the latter species.

Facultative reversal of the evolutionary trend from isophylly to heterophylly is rare in advanced groups of section *Cuspidata*, otherwise *S. novo-guineense* appears to be a neo-endemic derivative of *S. cuspidatulum*. Intermediate forms between these species have not been recorded anywhere in their combined geographical range (the single plant of *S. cuspidatulum* recorded from New Guinea, cited above, is quite typical in its anatomy), and the absence of *S. novo-guineense* from all other areas of the Malay Archipelago and Polynesia raises an obstacle to the view that the latter is a palaeoendemic form, perhaps ancestral to *S. cuspidatulum*.

Section C. *ACUTIFOLIA*

SPHAGNUM sect. ACUTIFOLIA Wilson, Bryol. Britt. : 20 (1855), excl. parte. – Schlieph. in Verh. zool.-bot. Ges. Wien 15 : 413 (1865).

Sphagnum (*Pycnosphagnum*) C. Muell. Hal. in Linnaea 38 : 545 (1874), *nom. nud.*
Sphagnum sect. *Mollia* W. P. Schimper, Syn. Musc. Eur., ed. 2 : 839 (1876), excl. parte.
Sphagnum sect. *Truncata* Husnot, Sphagnol. Eur. : 6 (1882).
Sphagnum 1. *Acuta* Lesq. & James, Manual Mosses N. Amer. : 12 (1884).
Sphagnum sect. *Pycnosphagnum* C. Muell. Hal. in Flora 70 : 404 (1887) ; Gen. Musc. frond. : 97 (1901).

Plants variable, usually medium-sized or rather small, occasionally almost as robust as subgenus *Sphagnum* ; secondary pigments nearly always present (except in conditions of dense shade), usually crimson, rarely brown or orange brown only (not in our area). Branches dimorphic, in fascicles of 4–5, rarely more. Cortical leucocysts of stem highly developed, in 3–4 layers, with or without pores in the outer walls. Branch-leaf leucocysts wide, strongly inflated (resembling subgenus *Sphagnum* anatomically), 20–35 μm or more ; dorsal surface with large ringed pores mainly in the cell angles, often appearing half-elliptic due to proximity with the commissures ; marginal rows of leucocysts on both surfaces with large, more or less free circular pores up to 20 μm or more diameter ; pseudolacunae often developed, generally less distinct than in subgenus *Sphagnum* but similarly disposed on the *dorsal* leaf surface (less strictly confined to the basal cell angles ; frequently undetectable in small-leaved boreal taxa). Chlorocysts in transverse section triangular or trapezoid with much wider exposure on the concave surfaces of the branch leaves, never immersed *sensu stricto* on the dorsal surface (Fig. 21, A).

Mainly northern hemisphere, hemiarctic to southern tropical (this range excludes the 'fimbriate' species *S. fimbriatum* Wils. and *S. girgensonii* Russ. which should probably be excluded from section *Acutifolia sensu stricto*), about 40–50 species.

For reasons stated above (p. 361) this section, which is fairly well circumscribed at least in the northern part of its range, is included here in subgenus *Isocladus*. Although the superficial resemblance, in the field, to sections *Subsecunda* and *Cuspidata* may be strong, its relationships, with the latter group at least, are not close. (Sections *Cuspidata* and *Acutifolia* probably represent two distinct and independent lines of development from a *Subsecunda* matrix.) On the other hand, similarities in structure between species of section *Acutifolia* and subgenus *Sphagnum* indicate a much closer phylogenetic proximity than hitherto realized. For example, the leucocyst anatomy, pore form and distribution (particularly the development of pseudolacunae) are such that separation of the two groups on leaf anatomy alone would be virtually impossible. There are parallels also to be drawn from among other features : the tendency to ventral displacement of the chlorocysts ; the multilayered cortex ; large-pored, amphiporous marginal zones in the branch leaves ; the occurrence of crimson pigments (although the latter have not been proven to be chemically identical).

15. ***Sphagnum junghuhnianum*** Dozy & Molk., Bryol. Jav. 1 : 27, t.18 (1854). (Text-figs 20 & 21.)

S. gedeanum Dozy & Molk., Bryol. Jav. 1 : 28, t. 19 (1854).
S. thomsonii C. Muell. Hal. in Linnaea 38 : 545 (1874) *'Thomsoni'*.
S. acutifolioides Warnst. in Hedwigia 29 : 192, t.4 f.4, t.7 f.16 (1890).
? *S. pseudomolle* Warnst. in Beih. bot. Zbl. 16 : 247 (1904).
? *S. kiiense* Warnst. in Engler, Pflanzenreich 51 (= Sphagnologia Universalis) : 82, t.24 F (1911).
S. junghuhnianum var. *gedeanum* (Dozy & Molk.) Warnst., tom. cit. : 116 (1911).
S. junghuhnianum var. *typicum* Warnst., loc. cit., *nom. invalidum*.
S. junghuhnianum var. *semiporosum* H. N. Dixon in J. Bot., Lond. 80 : 1 (1942).
S. squarrosiforme Dixon & Sherrin in H. N. Dixon, tom. cit. : 2 (1942).

Plants very variable ; pale and robust (resembling *S. squarrosum* Crome) varying to dense, small and compact (resembling *S. subnitens* Russ. & Warnst.), in the latter forms often appearing pale brownish but nearly always here and there with pale pink or reddish flecks (like the boreal *S. quinquefarium* (Braithw.) Warnst., never deep red as in *S. rubellum* Wils.). Stems pale to dark reddish brown, up to 1·2 mm diameter ; cortical leucocysts large and inflated, thin-walled, in 3–4 strata, without pores or very rarely with a single pore or thinning. Fascicles of 4(–5) branches ; branches usually strongly dimorphic, the 2–3 pendent branches colourless, more or less terete ; spreading branches 10–25 mm long. Stem leaves triangular lingulate, more rarely lingulate, exceptionally triangular and tapering from the base, (1·2–) 1·4–1·8–(2·1) mm long, 0·6–1·0 mm wide, typically fibrillose in the upper half, sometimes almost or quite to the base, more rarely almost or quite efibrose ; border narrow, only slightly expanded below ; ventral surface with few pores ; dorsal surface porose above and resembling the branch leaves (hemi-isophyllous forms) or with large resorption gaps which may be discrete, resembling unringed pores, or more or less confluent. Branch leaves large, normally five-ranked but not conspicuously so, 1·5–2·0(–2·5) mm long, (0·6–)0·7–1·0(–1·3) mm wide, oval-lanceolate,

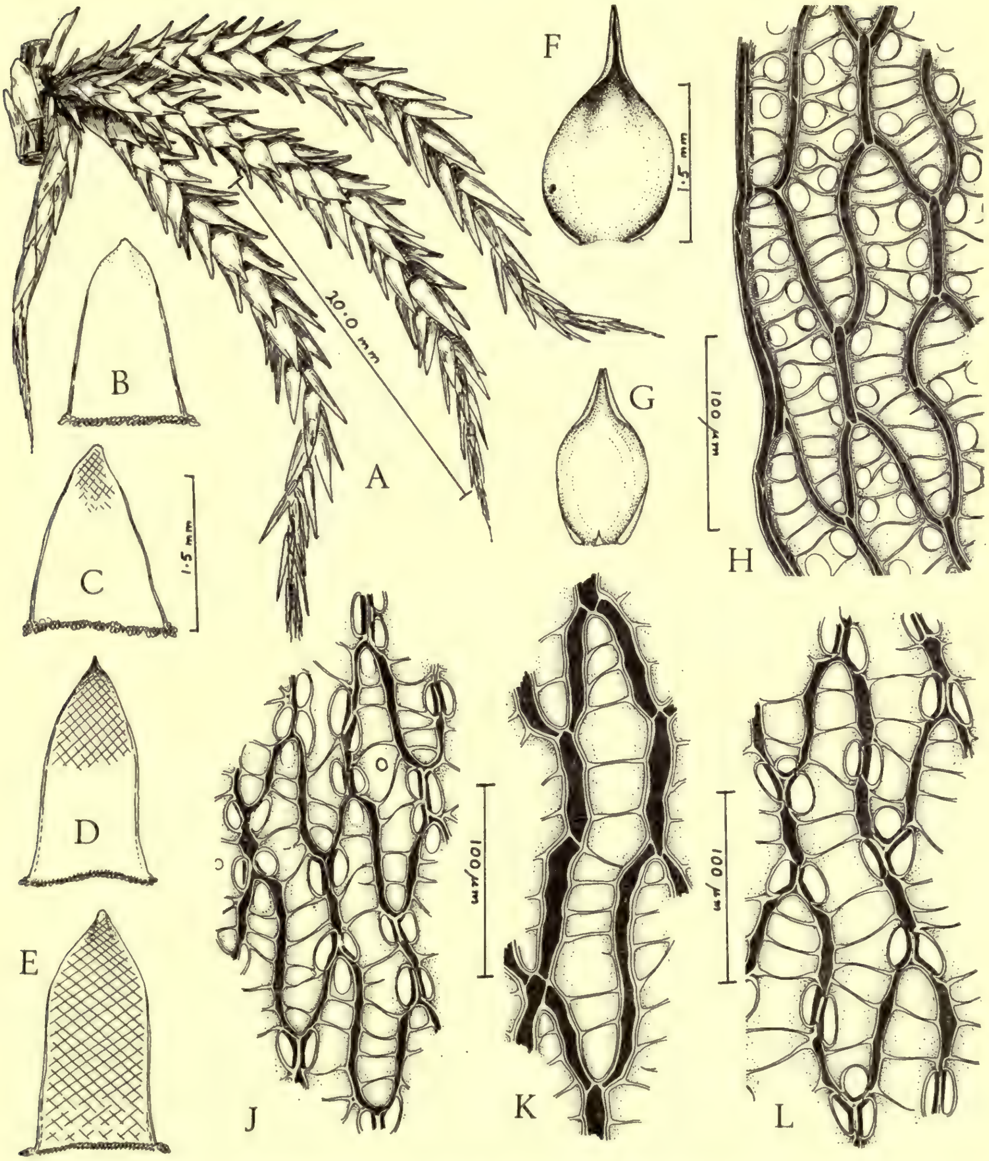

A
20.0 mm
B
C
1·5 mm
D
E
F
1·5 mm
G
H
100 μm
J
100 μm
K
100 μm
L

FIG. 20. *Sphagnum junghuhnianum* Dozy & Molk. : A, branch fascicle ; B, C, D, E, stem leaves ; F, G, branch leaves ; H, ventral leaf margin ; J, dorsal surface of branch leaf (near leaf apex) ; K, ventral surface of branch leaf (mid-leaf) ; L, dorsal surface of branch leaf (mid-leaf). (Stem leaves from various specimens, the remainder from *Eddy 4833*.)

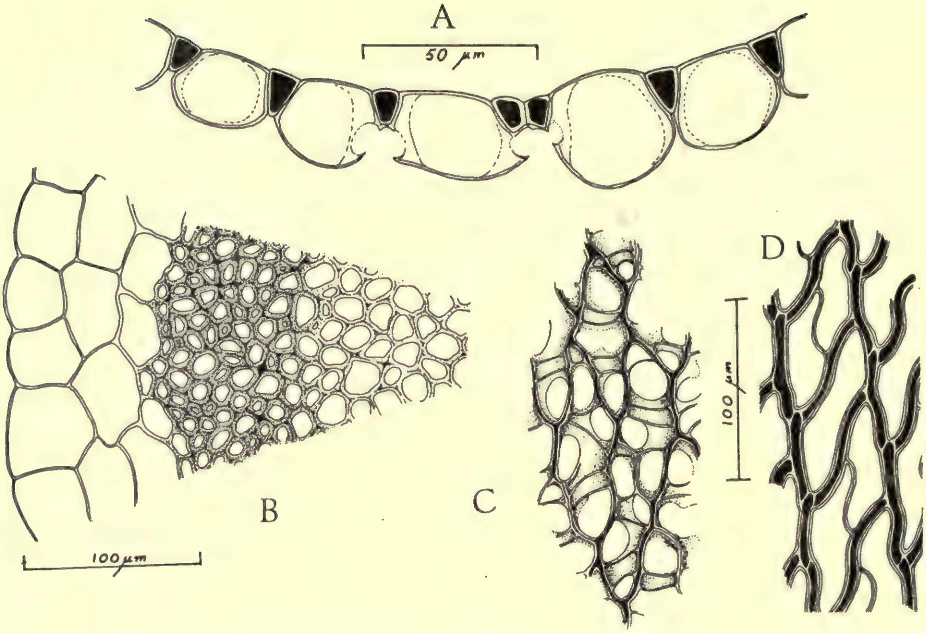
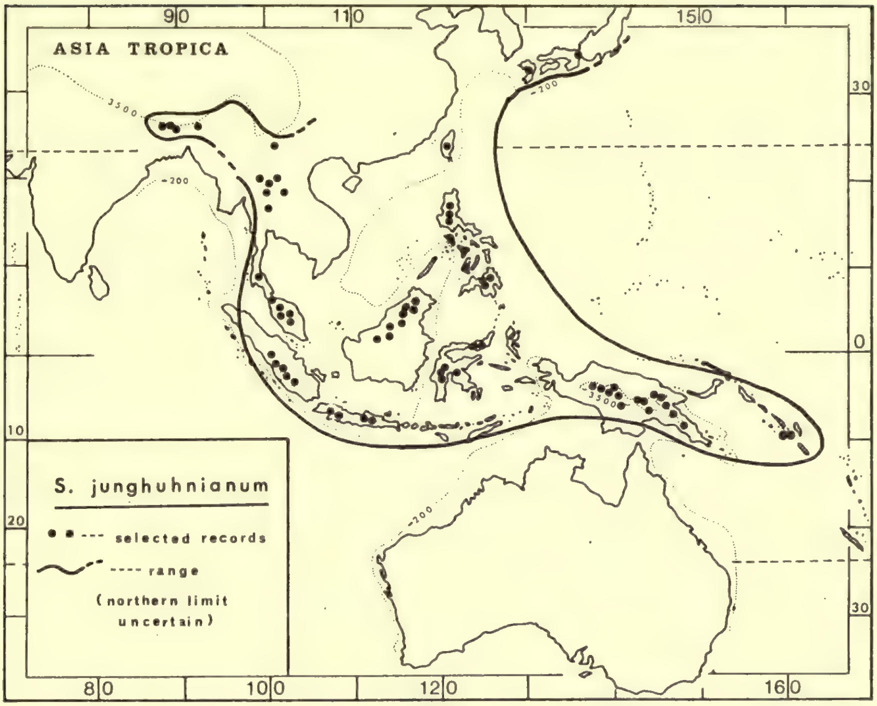


FIG. 21. *Sphagnum junghuhnianum* Dozy & Molk. : A, transverse section of branch leaf ; B, transverse section of stem ; C, stem-leaf areolation (fibrillose form) ; D, stem-leaf areolation (efibrillose form).

usually abruptly inrolled above and the upper part, reflexed or sub-squarrose, in compact forms the leaf tip slightly divergent ; apex truncate-dentate ; border without resorption furrow. Leucocysts in mid-leaf (i.e. base of limb) large and inflated, 25–35 µm wide, about 170 µm long ; dorsal surface of upper and mid-leaf with large, circular or half-elliptic ringed pores 12–20 µm diameter (smaller towards leaf apex, larger below) in the cell angles and here and there along the commissures (commissural pores of adjacent leucocysts often in opposed pairs), occasionally with additional free pores or an unringed resorption gap towards the apical angle ; ventral surface without or with relatively few pores ; a wide marginal zone in the lower half of the leaf (increasing downwards) with numerous large, ringed or unringed circular pores on both surfaces. Chlorocysts in transverse section triangular or more commonly trapezoid, thin-walled, with much wider exposure on the ventral leaf face.

Monoecious (autoecious) ; male bracts resembling the branch leaves but smaller (to 1·5 mm) ; female bracts large, 3·5 mm long, obtuse, convolute, mostly devoid of fibrils. Fruit typical of the genus. Spores tetrahedral, yellow, more or less smooth (light microscope), about 28 µm diameter.

Widespread in tropical and sub-tropical Asia eastwards from North East India, extending to New Guinea and adjacent islands, northwards to sub-tropical China and Japan. Locally frequent or abundant in the oceanic tropical zone above 2500 m alt. (Map 15).


ASIA TROPICA
S. junghuhnianum
● ■ --- selected records
---- range
(northern limit uncertain)
90
110
150
30
0
10
20
30
80
100
120
160
3500
200

MAP 15

INDIA: Khasia, *Hooker & Thomson 1293, 2082*; *J. D. Hooker 1288* (type collection of *S. thomsonii*, BM). Darjeeling, *Kurz 2082* (BM); *Decoly & Schaul s.n.* (BM).

THAILAND: Kanburi, *Kerr 141* (BM). Udawn, Touw *10863, 10970, 11066, 11067, 11068* (BM; L). Poo Kradeng, *Hansen et al., TDBS 6434, 6453, 6454, 6457* (C; L).

JAPAN: Ise, *Sasaoka 5083* (BM).

TAIWAN: *Sasaoka 5085*; *Faurie 218* (BM).

PHILIPPINES: Malabar, *Wallis s.n.* (BM). Mindanao, *Elmer 11369* (BM); *Merrill 11369* (BM); *Hachisuka 12, 13* (BM); *Robbins 4010* (L). Luzon, *Robinson 14052*; *Curran, Merritt & Zschokke 16421* (BM); *Elmer 8528, 22205* (L); *Ramos 7315* (BM); *Clemens 9341* (L); *Loher 1046*; *Merrill 4919, 4920, 4869, 8528*; *Van Royen 5621* (L). Negros, *Edano 21934* (L). Mindoro, *Merrill 5707* (BM; L).

MALAYA: Kedah, *Spare 2871* (BM); *Holttum 14882a* (SING); *25341* (BM). Kelantan, *Nur 12243* (SING; BM). Pahang, *Robinson 5435* (BM); *Spare 3333, 3573* (BM); *Holttum 20905, 20907, 20914, 20918, 21561, 23529,* (BM; SING); *Burkill 2379* (BM); *Ridley 1038, 1908* (SING); *Henderson 17877a* (BM); *Inoue s.n.* (BM). Perak, *Ridley 22* (BM; SING). Selangor, *Ridley 277* (BM; SING).

SUMATRA : G. Goh Lemboek, *Van Steenis 10223* (BM ; L), *4063* (L). Penhoeloe Bao, *Frey-Wyssling 41* (BO). Mt Sago, *Meijer 6058, 6096, 6807, 6820, 7150* (L). Mt Singgalang, *Meijer 6393* (BM).

JAVA : G. Patoeh, *Junghuhn* (holotype, L) ; *Blume* (L) ; *Reinwardt* (L). G. Gede, *Teysmann* (type collection of *S. gedeanum*, L). Tjibodas Forest Reserve (Gede and Pangrango), *Fleischer, Krypt. Exsicc, 1589* ; *Musc. Fr. Arch. Ind. 2* ; *501* (BM) ; *Kurz 670, 847* (BM) ; *Hasskarl s.n.* (L) ; *De Vriese s.n.* (L) ; *Van den Bosch, Bry. Jav. 18, 19* (BM ; L) ; *Verdoorn 65* (BM) ; *Van Steenis 11156* (L) ; *Van Der Wijk 1087* (L) ; *Eddy 4030, 4134, 4377, 4398* (BM). Priangan, *Verdoorn, Musc. Sel. Crit. 45* (L) ; *Van Steenis 4291* (L). G. Patoeh, *Van Steenis 4429, 6920, 6921* (L).

BORNEO : *Beccari s.n.* (BM). Kinabalu, *Gibbs 4145* (BM) ; *Holttum 25341* (BM), *25466* (SING) ; *Meijer 12641, 62715* (L). Sarawak, *Oxford Expedition, (1932) 2730* (BM). Santubong, *Richards 5700* (L).

SULAWESI : Menado, *Bloembergen 2947* (L). Porema, *Kjellberg 79* (BM) ; *Bunnemeijer 11968* (BM). Latimojong, Pokapindjang, *Eyma 825* (L) ; *Bunnemeijer 1672* (L) ; *Eddy 4830, 4833, 4748, 5008* (BM).

NEW GUINEA : West Irian, Arfak Mts, *Gibbs 5967* (BM) ; *Brass & Meyer-Drees 9738* (BO) ; *Sleumer & Vink 4275* (BM). Kebor Valley, *Van Royen 3878* (L). New Guinea, Mt Giluwe, *Schodde 1897, 1901* (BM). Matate-Lala Divide, *Carr 15024* (holotype of *S. junghuhnianum* var. *semiporosum*, BM), *15198* (holotype of *S. squarrosiforme*, BM). 'N. Guinea', *H.R.H. Prince Leopold 1* (BM). *Clemens 4105* (BM). Mt Kaindi, *Streimann, NGF 44452* (L) ; *Eddy 1b, 175* (BM). Papua, *Pullen 5944* (BM). Mt Awormange, *Van Royen NGF 20380* (L). Mt Piora, *Womersley NGF 19029* (BM ; L). Cromwell Mts, *Hoogland 9583, 9550* (BM ; L). Sarawaket Range, *Hoogland 9962* (L). Mt Enggom, *Van Royen, NGF 16197* (BM). Wonemara, *Robbins 4169* (L). Western Highlands, *Hoogland & Schodde 6982, 7501, 7163, 7630* (BM). Mt Hagen, *Van Zanten 68306, 68890* (L). Central Highlands, Kadubaka, *Bergman 48* (L). Huon Peninsula, Finisterre Range, *Eddy 1023, 1134* (BM). Mt Abilala, *Eddy 1256, 1262* (BM). Central Highlands, Mt Elandora, *Eddy 2109a* (BM). Mt Wilhelm, *Eddy 2564, 2576* (BM).

SOLOMON ISLANDS : Guadalcanal, *Robbins 4334* (L) ; *Van Zanten 682607, 682620, 682711, 682714* (BM ; GRO) ; *Dennis 20038, 20041* (BM).

Sphagnum junghuhnianum is perhaps the most abundant and widespread species of the genus throughout tropical Asia. Ecologically it appears to be mainly a plant of wet ground in open forest at medium to high altitudes, often associated with *S. cuspidatulum* or *S. sericeum*. Response to environmental conditions is reflected largely in the vigour and colour of the plant. Luxuriant forms, such as those from the hot-springs area and waterfalls on Mt Gedeh in Java, resemble *S. squarrosum* in habit and have customarily been named *S. junghuhnianum* var. *gedeanum*. At the other extreme, small clumps of a pale brownish hue are to be commonly seen in open forest with a tendency to fluctuating rainfall, especially above 3500 m alt., in higher light intensity. Plants of the latter form are abundant in the Latimojong

Mountains of South Sulawesi, but clumps in favoured sites showed every gradation to the '*gedeanum*' type. Structural variation is confined mainly to the extent of fibrillation and dorsal leucocyst wall resorption in the stem leaves. Apart from ecological variants, there do not seem to occur races which can logically be distinguished as varieties or subspecies, at least within the area under consideration.

Suzuki (1956) distinguishes two subspecies of *S. junghuhnianum* : subsp. *junghuhnianum* and subsp. *pseudomolle* (Warnst.) Suzuki, separated principally on the distribution of stem-leaf pores. Furthermore, he excludes subsp. *junghuhnianum* from Japan and Taiwan. My own investigations among tropical gatherings of *S. junghuhnianum* failed to convince me that, within the extensive variation of stem-leaf morphology encountered, any clear-cut division into subspecific taxa on that basis was supportable. Perhaps a distinct genotype can be isolated among plants from more temperate latitudes (Suzuki's conclusions were based largely on Japanese material) but a subsequently wider occurrence of subsp. *pseudomolle* in tropical Asia, reported by Suzuki (1966), implies a geographical range largely coincident with that of subsp. *junghuhnianum*. Under the circumstances I do not feel that, what appears to be artificial, splitting of *S. junghuhnianum* is justifiable within our area.

Gangulee (1970) describes the stem cortex as being uniporose, a character that Warnstorf mentioned in his description of his *S. acutifolioides* (= *S. junghuhnianum*). Such cortical pores are generally rare in this species, and even when present are of very sparing occurrence.

No other species of section *Acutifolia* are known from tropical Asia so that confusion is unlikely. *S. subnitens*, a widespread and locally abundant species in the northern hemisphere, is closely related to *S. junghuhnianum* and closely resembles compact forms of the latter. It lacks, however, the 5-ranked branch-leaf arrangement, has smaller, non-squarrose leaves and different spore morphology (larger, darker, more papillose).

The names *S. junghuhnianum*, *S. gedeanum* and *S. hollianum* (see p. 437) are normally cited as having been published in Dozy's paper on the anatomy and phytogeography of *Sphagnum* published in the *Verhandelingen* of the Amsterdam Academy (Dozy in *Verh. K. Akad. Wet., Amst.* 2(3) : 3–11, t.1–2 (1854)). However, although these names are mentioned and there are figures of details of their leaves, there is nothing that amounts to a diagnosis or description, and the illustration of the microscopic features of the leaf can hardly be regarded as a 'figure with analyses'. Accordingly, if Dozy's paper was published earlier in 1854 than the fourth fascicle of the *Bryologia Javanica*, which included pp. 27–29, the names there were *nomina nuda*.

Subgenus ***RIGIDA***

SPHAGNUM subgenus RIGIDA (Lindb.) A. Eddy, stat. nov.

Sphagnum B. *Heterophylla* b. *Rigida*. Lindb. in Öfvers. K. VetenskAkad. Förh. Stockh. 19 : 135 (1862), excl. parte.

Sphagnum 4. *Rigida* (Lindb.) Schlieph. in Verh. zool.-bot. Ges. Wien 15 : 413 (1865), excl. parte. – Lindb., Musci Scand. : 11 (1879).

Sphagnum III. *Truncata* Russow, Beitr. Kenntn. Torfmoose : 32, 74 (1865), reimpr. in Arch. Naturk. Liv.-Est. u. Kurlands, ser. 2, 7 : 112, 154 (1867), excl. parte.
Sphagnum sect. *Mollia* W. P. Schimper, Syn. Musc. Eur., ed. 2 : 839 (1879), pro parte.
Sphagnum sect. *Malacosphagnum* C. Muell. Hal. in Flora 70 : 404 (1887) ; Gen. Musc. Frond. : 97 (1901).
Sphagnum A. *Litophloea* sect. *Rigida* Warnst. in Hedwigia 33 : 319 (1894).
Sphagnum 5. *Compacta* C. Jensen, Danm. Mosser : 291 (1915).

Type : *S. rigidum* (Nees & Hornsch.) W. P. Schimp. = *S. compactum* DC.

Plants normally robust, resembling subgenus *Sphagnum* or the boreal section *Squarrosa* ; pale greenish, fuscous or bright orange-brown, seldom or perhaps never with crimson pigmentation. Stem cortex well developed ; cortical leucocysts in 3–4 layers, mostly uniporose, efibrose. Branches strongly dimorphic. Stem leaves much reduced (isophyllous forms very rare) relative to the size of the branch leaves, 0·5–1·0(–1·8, Australasia) mm long. Branch leaves large, ovate, apex widely truncate-dentate ; border narrow, usually with resorption furrow ; leucocysts wide and relatively short (cf. subgen. *Sphagnum* but less strongly inflated), 35–45 μm wide. Pores, when present, relatively small, ringed or unringed, 10·0–15·0 μm diameter. Pseudolacunae very well developed, confined to the *ventral* leaf surface at the conjunction of the basal and lateral convergence of three adjacent leucocysts (cf. sugben. *Sphagnum*). Chlorocysts narrow, in transverse section with oval lumen and more or less incrassate walls, central and completely enclosed or displaced towards the dorsal leaf surface where they may appear narrowly exposed via their highly refractive posterior walls.

Geographical range of the genus. Three or possibly four species.

From a phylogenetic standpoint, the position and status of this group has posed many problems. Lacking a number of the diagnostic features of subgenus *Sphagnum* (with which, prior to 1860, on account of its robust size and large branch leaves, it had sometimes been included), it was nevertheless considered by most sphagnologists to be somehow distinct from subgenus *Isocladus*. Consequently, common practice has been to create or maintain a distinct section to accommodate it, although no good single diagnostic feature had been described to support such a treatment ; Andrews' (1937) claim that the perichaetial leaves are unique is questionable. Distinctions of a quantitative nature could not be used alone to support the treatment of the group as a subgenus and Isoviita (1966 : 230) was justified, on the basis of the information then available, in his statement regarding the status of *Rigida*. Now that the presence of pseudolacunae in *Rigida* has proved to be constant, their position on the ventral leaf surface being unique, I feel justified in restoring to *Rigida* the rank of subgenus.

The presence of the pseudolacunae, while solving to some extent the problem of the status of the taxon, poses others. Of precisely the same structure as those in subgenus *Sphagnum*, their position on the opposite surface of the leaf is perplexing. A proximity of relationship with the latter group has frequently been suggested, and there are striking similarities of distribution within these subgenera. Like subgenus *Sphagnum*, subgenus *Rigida* contains comparatively few species, including one which is pan-tropical. Furthermore, each has a single distinct Australasian representative, and each achieves greatest diversity in the north temperate zone, particularly in North America. However, the differences between the two subgenera are too fundamental and I incline to regard as most probable an early segregation from a branch of section *Subsecunda* (probably a group containing forms similar to *S. robinsonii*), subsequent development taking place along somewhat parallel lines to subgenus *Sphagnum*.

16. ***Sphagnum strictum*** Sullivant, Musci Allegh. : 49 (1846).

16a. Subsp. ***strictum***. Not present in tropical Asia.

16b. Subsp. ***pappeanum*** (C. Muell. Hal.) A. Eddy, comb. nov. (Text-figs 22 & 23.)

S. pappeanum C. Muell. Hal., Syn. Musc. Frond. 1 : 101 (1848).
S. domingense C. Muell. Hal. in Hedwigia 37 : 219 (1898).
S. antarcticum Mitten, *sensu* Bartram in Lloydia 5 : 246 (1942), non Mitten.

Plants very variable in stature, short and dense or laxer and approaching subgenus *Sphagnum* in habit; pale straw-coloured or greenish. Stem pale, yellowish to yellow-brown, about 0·9 mm diameter; cortex well developed, leucocysts in 2–3 layers, the outer series about 40 μm wide, efibrose and mostly with a single pore. Fascicles of 5–6 branches, 2–3 spreading branches usually short, up to 12·0 mm long, pendent branches caudiform, weak and appressed to stem (i.e. branches strongly dimorphic). Stem leaves small, (0·7–)0·8–1·0 mm long, 0·6–0·8 mm wide, widest at insertion, triangular with rounded, erose-dentate or erose-fimbriate apex; fibrillose at least near apex and sometimes to below the middle; resorption gaps numerous on the ventral surface; dorsal surface more or less eporose; border present but indistinct, somewhat expanded to about 7–8 cells width. Branch leaves large, 2·5–3·0 mm long, ovate and wide at apex but appearing narrowed above due to the strongly inrolled margins, usually patent above from a suberect base and often appearing subsquarrose; apex truncate-dentate; border of a single cell width, with a resorption furrow. Leucocysts wide, 30–35 μm in mid-leaf, 110–160 μm long; dorsal surface usually with few true pores but with numerous pseudopores, the latter often in short series along the mid-lateral commissures; ventral surface of leucocysts usually eporose for the most part, or pores rare, but pseudolacunae constantly present and reasonably conspicuous. Normal pores, relative to the dimensions of the leucocysts, small, 11–12 μm diameter. Chlorocysts narrow, in transverse section with narrow, oval lumen, more or less completely enclosed or just emergent on the dorsal surface via the strongly thickened postical wall. Commissural walls papillose. Fertile material not known from tropical Asia; female bracts (African material) large, 3·0–4·0 mm long, sheathing; basal cells prosenchymatous and more or less uniform; upper cells resembling those of the branch leaves. Spores not seen.

Pan-tropical with wide disjunctions; Africa (main occurrence), Malaysia (New Guinea and Sulawesi), Central America (Map 16).

AMERICA: Guadelupe, Cose de la Soufriere, *Verguiel s.n. (1902)* (L); *Pfiffer 218* (BM). San Domingo, *Eggers 2054* (type collection of *S. domingense*, BM). Mexico, Galeotti 6879 (BM).

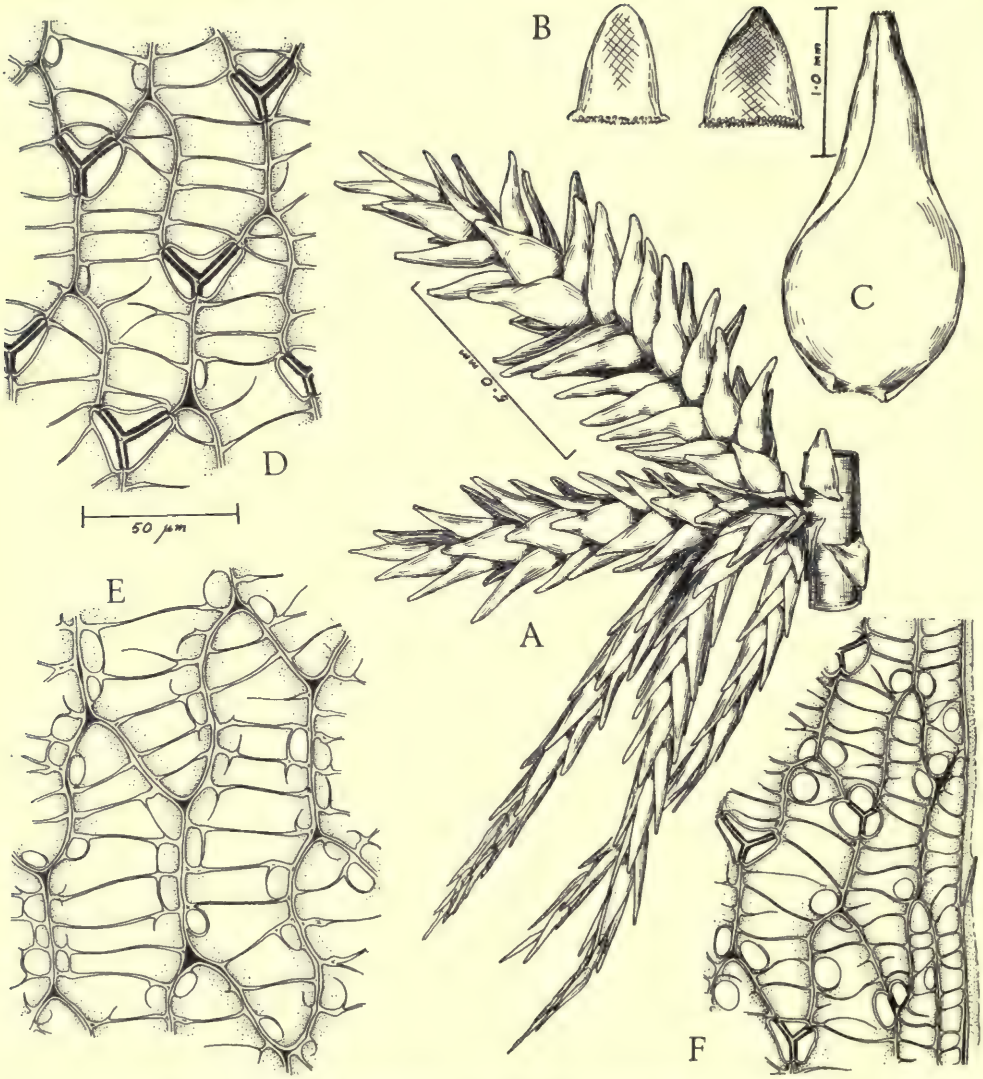


FIG. 22. *Sphagnum strictum* Sull. subsp. *pappeanum* (C. Muell. Hal.) A. Eddy : A, branch fascicle ; B, stem leaves ; C, branch leaf ; D, ventral surface of branch leaf ; E, dorsal surface of branch leaf ; F, ventral surface of branch leaf (marginal). (All drawn from *Brass & Meyer-Drees 9737*.)

AFRICA : South Africa, *Ederhuysen 15049* (BM) ; *Rehmann 12* (BM) ; *Sim 9261* (BM) ; *Wager 568* (BM). East Africa, *Balbo 334, 352* (BM) ; *Thomas 2446* (BM) ; *Wood 1090* (BM) ; *Taylor 1976, 2986* (BM) ; *Mearns 1562* (BM) ; *Stuhlmann 2385* (BM). East African Islands, Bourbon, *Rodriguez* (BM) ; Reunion, *Lepuranche* (BM).

SULAWESI : Pokapindjang, *Eyma 605* (L) ; *Eddy 4831b* (BM).

NEW GUINEA: Mt Wilhelmina, *Brass & Meyer-Drees* 9737 (BM; BO).

The close relationship between *S. pappeanum* C. Müll. and *S. strictum* Sull. was mentioned by Andrews (1941a) and later by Taylor & Thompson (1954). Some African populations, being exceptionally robust, have a superficial aspect which is markedly different from the Asiatic plants. Less robust forms, more closely resembling the Asiatic specimens and *S. strictum* subsp. *strictum*, are equally common in Africa, and there are no grounds for the separation of the Asiatic or American forms from *S. strictum* subsp. *pappeanum*. Hitherto, all Central American forms have been referred to *S. strictum* subspecies *strictum* but the minor anatomical details which distinguish subspecies *pappeanum* are clearly represented in the above-cited specimens. The gatherings from Guadelupe, in particular, approach the more robust facies familiar among African populations.

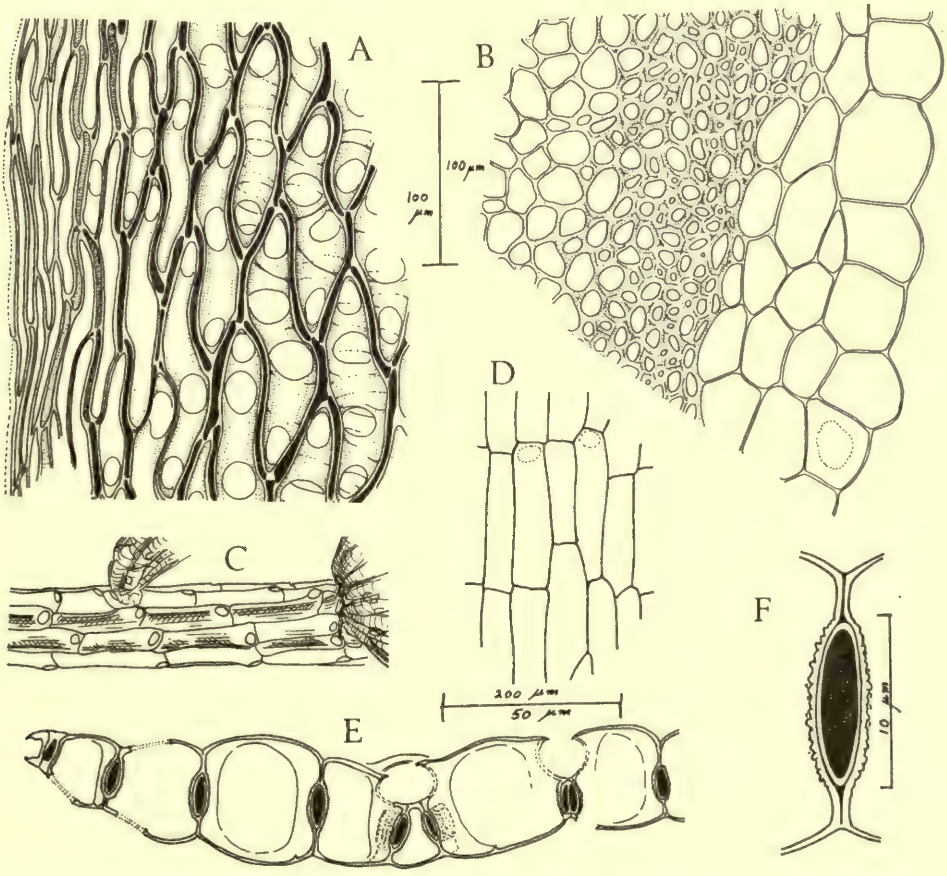
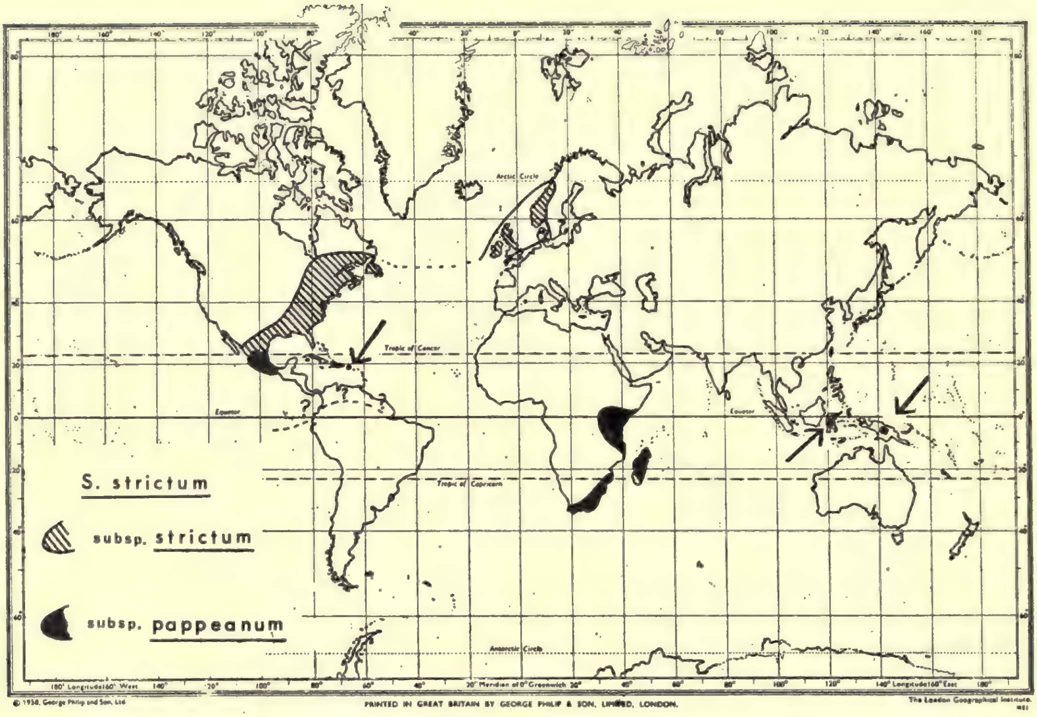


FIG. 23. *Sphagnum strictum* subsp. *pappeanum* (C. Muell. Hal.) A. Eddy: A, part of stem leaf (marginal); B, transverse section of stem; C, part of branch; D, stem-cortex; E, F, transverse section of branch leaf. (Drawn from *Brass & Meyer-Drees* 9737.)


S. strictum
subsp. strictum
subsp. pappeanum
Arctic Circle
Tropic of Cancer
Equator
Tropic of Capricorn
Antarctic Circle
180° Longitude 160° West
Meridian of 0° Greenwich
140° Longitude 160° East
© 1958. George Philip and Son, Ltd
PRINTED IN GREAT BRITAIN BY GEORGE PHILIP & SON, LIMITED, LONDON.
The London Geographical Institute

MAP 16

Bartram (1942, *loc. cit.*) identified the New Guinea plant with the Australasian *S. antarcticum* Mitt., to which it bears strong resemblance, and was probably influenced by the proximity of New Guinea to Australasia and the absence of any other species of subgenus *Rigida* from tropical Asia.

Subspecies *pappeanum* differs from typical subsp. *strictum* only in minor quantitative characteristics. Its stem leaves are larger on average than in the latter, and are usually fibrillose in the upper third. There is an associated tendency for more complete enclosure of the chlorocysts and rather coarser papillation of the commissural walls. The distinguishing features of the subspecies, although slight, seem to be fairly constant in tropical populations. Quantitatively, they would scarcely seem to merit more than varietal weighting. However, the rank of variety in *Sphagnum* has been so arbitrarily applied that I prefer to avoid the application of that rank to taxa which exhibit correlated distribution patterns.

S. antarcticum, which is usually more robust, differs mainly in its darker stems and rectangular, truncate and erose or fimbriate stem leaves.

Subgenus ***HOMOPHYLLA***

SPHAGNUM subgenus HOMOPHYLLA (Lindb.) Wijk, Margadant & Florschütz in Regnum veg. 48 (= Index Muscorum 4) : 406 (1967).

Sphagnum A. *Homophylla* Lindb. in Öfvers. K. VetenskAkad. Förh. Stockh. 19 : 134 (1862).

Sphagnum sect. *Homophylla* (Lindb.) Braithw. in Mon. microsc. J. 7 : 55 (1872).

Sphagnum sect. *Acocosphagnum* C. Muell. Hal. in Flora 70 : 405 (1887) ; Gen. Musc. frond. : 97 (1901). – Isoviita in Annls. bot. fenn. 3 : 255 (1966).

Sphagnum sect. *Cuspidata* A. *Efibrosa* (a) *Sericea* Warnstorf in Hedwigia 29 : 214 (1890).

Sphagnum sect. *Sericea* (Warnst.) Fleischer, Musci Fl. Buitenz. 1 : 4 (1904).

Type : *S. sericeum* C. Muell. Hal.

Plants isophyllous, the stem leaves differing from the branch leaves only in the wider insertion. Leaves contracted abruptly at apex to a distinct mucro, never eroded or truncate-dentate. Leucocysts of leaves devoid of fibrils, normally with a single, rather large and sometimes protuberant pore in the apical angle (Fig. 24, E, F) on the outer or both surfaces. Structure of stem and branches as in section *Cuspidata*. Chlorocysts in section more or less rectangular, scarcely displaced.

Represented by a single species, confined to the Malay Archipelago, from the Malay Peninsula to New Guinea.

16. ***Sphagnum sericeum*** C. Muell. Hal. in Bot. Ztg. 5 : 481 (1847). (Text-fig. 24, Pls 39, F & 40, A.)

S. hollianum Dozy & Molk., Bryol. Jav. 1 : 29, t.20 (1854) – Dozy in Verh. K. Akad. Wet., Amst. 2(3) : 5, t.2 f.12–13 (1854). (See note, p. 431 above, on publication of *S. junghuhnianum* and *S. gedeanum*.)

S. seriolum C. Muell. Hal. in Flora 70 : 421 (1887).

Plants medium-sized or rather small, light green or pale yellowish green, with a silky lustre especially when dry. Stem 0·4–0·8 mm diameter ; internal cylinder pale brown or yellowish ; cortical leucocysts distinct, about 40 μm wide, in two layers, without pores. Fascicles of 4–8 branches which are monomorphic, 8·0–20·0 mm long. Branch cortex with distinct retort cells as in subgenus *Isocladus*. Stem leaves 0·7–1·0(–1·2) mm long, 0·7–0·9 mm wide, oval-triangular, apiculate ; border narrow, not expanded below ; areolation identical throughout to that of the branch leaves. Branch leaves uniform in size along the branch, 5-ranked, concave, lending to the branches a julaceous or beaded appearance, abruptly tapering or more usually apiculate, never truncate-dentate, 0·8–1·2 mm long, 0·6–0·8 mm wide ; border narrow, 1–2 cells wide, denticulate, confluent above to form the apiculus at apex in which there is no trace of resorption, sometimes a considerable area of apical tissue made up of uniformly prosenchymatous cells. Leucocysts shortly vermicular (lateral angles scarcely developed), 10–15 μm wide, without any trace of fibrils and usually with a solitary large, often protuberant pore in the apical angle on one or both surfaces (less commonly eporose, rarely with a small resorption gap in the basal angle). Chlorocysts widely exposed on both surfaces, in section rectangular or trapezoid, centrally placed or slightly wider ventrally, walls somewhat thickened.

Monoecious but rarely fruiting ; male bracts hardly distinguishable from normal branch leaves ; female bracts to 3·5 mm long, acute or apiculate, convolute and sheathing. Spores tetrahedral, yellow, smooth, 25–28 μm diameter.

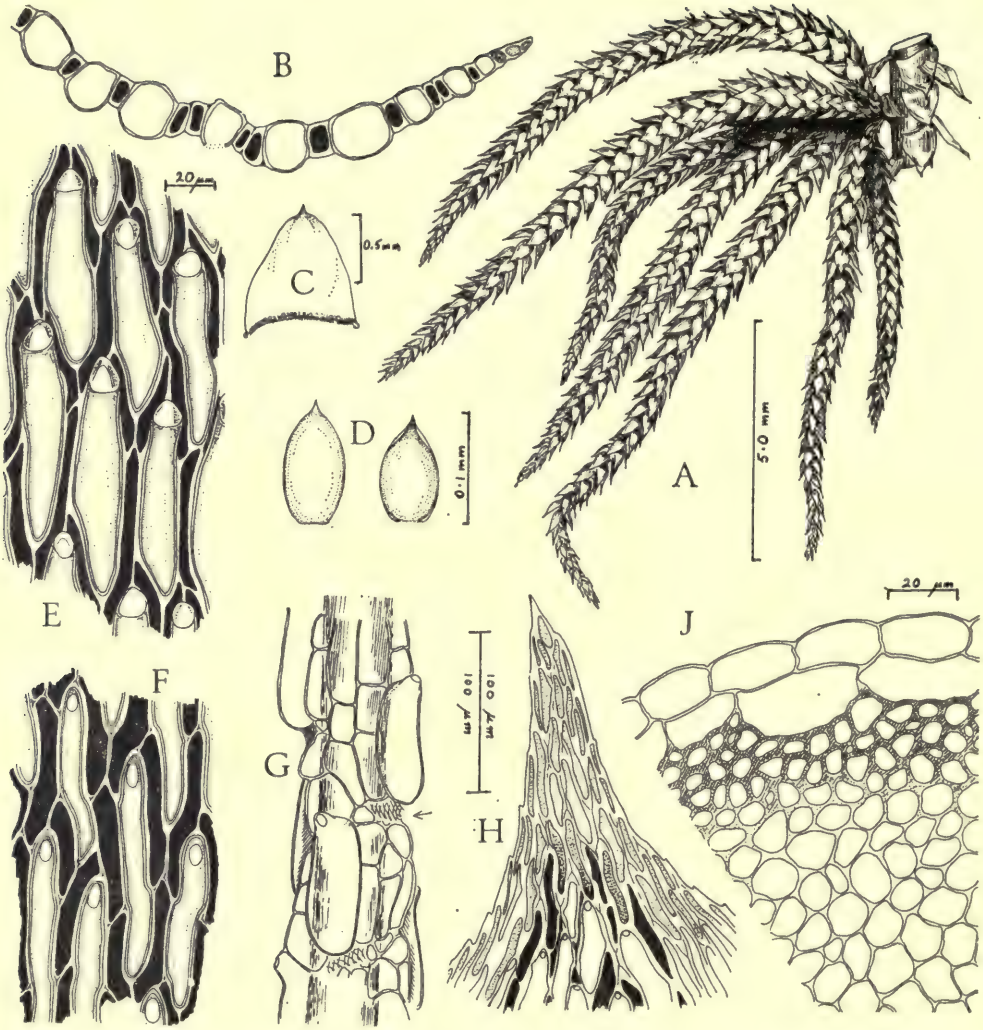


Fig. 24. *Sphagnum sericeum* C. Muell. Hal. : A, branch fascicle ; B, transverse section of branch leaf ; C, stem leaf ; D, branch leaves ; E, F, dorsal surfaces of branch leaves ; G, defoliated branch ; H, apex of branch leaf ; J, transverse section of stem. (A, E, G, drawn from *Eddy 4024*, the remainder from *Bry. Jav. 20*.)

Malay Peninsula to New Guinea ; locally frequent at moderate to high altitudes in open rain forest and beside waterfalls (Map 17).

Malaya : Pahang, *Holttum 20911, 23530* (BM ; SING).

Sumatra : Gunung Lubu Radja, *Junghuhn* (type collection of *S. sericeum*, Herb. Schimper, BM, Herb. Hampe. BM ; L). Mt Singgalang, 1878 (BM); *Beccari s.n. 1878* (Isotype of *S. seriolum*, L) ; *Meijer 6143, 9552, 9642, 9697, 11038, 11706* (L). Mt Sago, *Meijer 6828* (BM ; L). Sibajak, *Haal 261* (L).

Java : Mt Salak, *Holle* (holotype of *S. hollianum*, L) ; *Zollinger 2217* (L) ; *Hochreutiner 2069* (L) ; *Van Steenis 12368* (L). *Bry. Jav. 20, 21* (BM ; L). Tjibodas Forest Reserve, Gede and Pangrango, *Fleischer, Musc. Fr. Arch. Ind. 3* (BM) ; *Krypt. Exsicc. 1291* (BM) ; *Meijer 3447* (L) ; *Van Steenis 2136* (L) ; *Van der Vijk 1095* (L) ; *Eddy 4316d, 4369c* (BM).

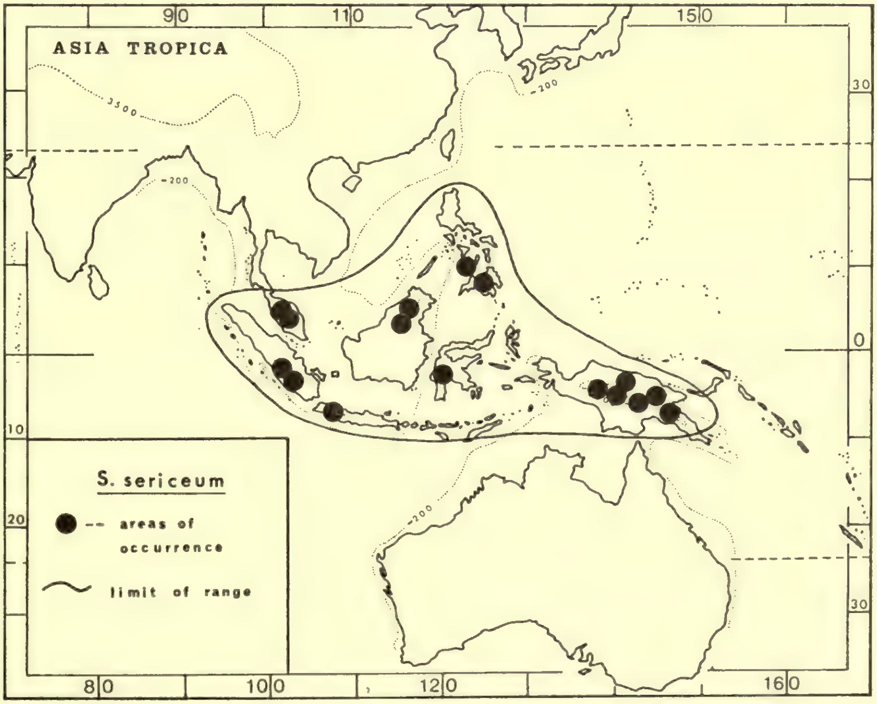
Philippines : Mindanao, *Elmer 11369* (BM). Negros, *Edano 20189* (BM ; L).

Borneo : Kinabalu, *Gibbs 4145* (BM) ; *Meijer 11127* (L). Koemoel, *Brocksmit 4530* (L). Mt Mulu, *Hose 2* (BM). Maraparai Ridge, *Holttum 25622* (BM). Sarawak, Mt Dulit, *Oxford Expedition (1932) 2095, 2185* (BM).

Sulawesi : Pokapindjang, *Eddy 4701* (fert., BM).

New Guinea : Cyclops Mts, *Van Royen 3718* (BM). Idenburg River, *Brass 12175* (BO). Wabag, *Robbins 2866, 3358* (LAE). Owen Stanley Range, *Robbins 4241* (L). Mt Hagen, *Hoogland & Pullen 5931* (BM). Port Moresby, *Carr 15190* (BM). Edie Creek, *Eddy 104b* (BM). Mt Kaindi, *Van Zanten 68274* (BM ; GRO). Schrader Range, *Robbins 3936* (L). Finisterre Range, *Eddy 1150b, 1502* (BM). Mt Wilhelm, *Eddy 2901b* (BM). Mt Otto, *Argent, NGBF 8/7/71, nos. 97, 123* (BM). Sepik District, *Hoogland & Craven 11006* (L).

Sphagnum sericeum is readily identifiable, possessing a combination of characters unique among the Sphagnales, which could well form the basis of a distinct genus.



Map 17

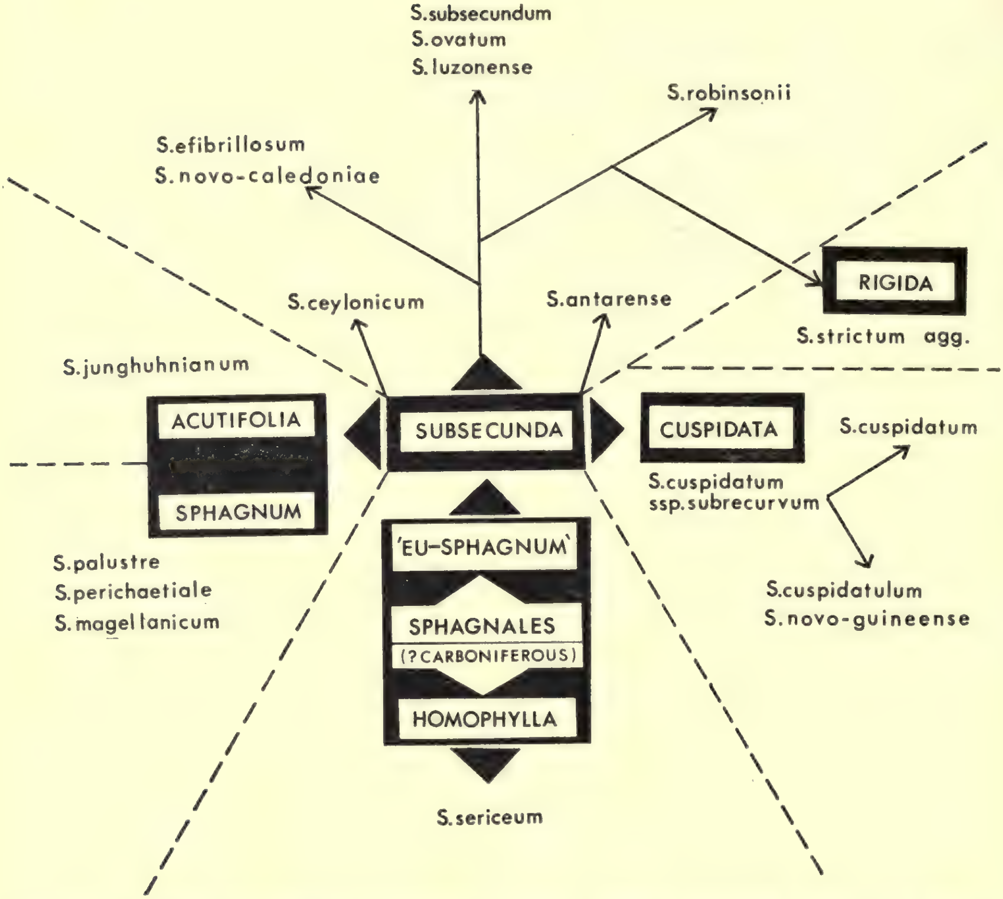

S.subsecundum
S.ovatum
S.luzonense
S.robinsonii
S.efibrillosum
S.novo-caledoniae
RIGIDA
S.ceylonicum
S.antarense
S.strictum agg.
S.junghuhnianum
ACUTIFOLIA
SPHAGNUM
SUBSECUNDA
CUSPIDATA
S.cuspidatum
S.cuspidatum ssp.subrecurvum
'EU-SPHAGNUM'
S.palustre
S.perichaetiale
S.magellanicum
SPHAGNALES
(?CARBONIFEROUS)
HOMOPHYLLA
S.cuspidatulum
S.novo-guineense
S.sericeum

FIG. 25. Suggested phylogeny of tropical Asiatic *Sphagna*. Broken lines divide major subgeneric groups; solid triangles indicate early divergences of main subgenera, arrows indicate probable trends within them.

The most obvious feature, the lack of fibrils in the leucocysts, is to be found very rarely in other *Sphagna* and this led Warnstorf to place *S. sericeum* with species belonging correctly to section *Subsecunda*. There are, however, no other grounds for including this species with any other section. Anatomical features of stem and branch resemble those of section *Cuspidata*, but the ventral displacement of the chlorocysts in conjunction with other characters are far removed from that group.

The absence of fibrils in the leucocysts of *S. sericeum* is a primary feature, in my opinion, not a secondary reduction as in *S. macrophyllum*. The non-resorption of the leaf apices should be similarly regarded, and this feature should be emphasized, having received little or no attention in the past. In a number of specimens (especially marked in the Mt Otto material) the differentiation of chlorocyst and leucocyst may be slight in the apical region of the leaf, sometimes the whole apical tissue being prosenchymatous. Persistence of the primitive state, rather than suppression of an 'advanced' modification of leaf apex is indicated, which, taken in conjunction with other features, demonstrates the antiquity of the species.

The distribution of this subgenus is something of a paradox. There is evidence, albeit circumstantial, supporting the view that the sections and subgenera of *Sphagnum* are of great antiquity, and that diversification has been exceedingly slow. From that viewpoint, a region of comparatively recent geological origin and isolation, allowing for the usual endemic species of more or less obvious derivation, would not be expected to contain an endemic subgenus. There seems to be no very obvious reason for the comparative lack of success in geographical extension of range of this subgenus which does not seem to differ significantly in its ecology from, e.g., *S. junghuhnianum* (but restriction of range to single, or widely disjunct localities is a well-documented feature of very old taxa). Possibly, lacking fibrils, and consequently restricted in leucocyst enlargement, *S. sericeum* is less able to cope with climatic variation or periods of slight dessication.

Taxa excluded

Section *Squarrosa* (Russ.) Schimp.

H. N. Dixon in his description of *Sphagnum squarrosiforme*, included it in the small section *Squarrrosa*, thus extending the range of this boreal group to New Guinea. *S. squarrosiforme* is merely a partially aberrant gathering of *S. junghuhnianum* (sect. *Acutifolia*) in which many chlorocysts lack cell contents and have collapsed. Section *Squarrosa* is therefore excluded from the tropical zone.

Sphagnum borneoense Warnstorf in Allg. bot. Z. 1 : 229 (1895).

Warnstorf's original description was based on packing material sent from, and presumably returned from, Borneo. He compared it to *S. papillosum*, a species confined to the temperate northern hemisphere, to which LeRoy Andrews rightly reduced it later (1951). In any case the origin of the type collection was always in doubt. The identification of a second specimen with *S. borneoense*, a specimen moreover of undoubted origin (*Nur 2236*), seemed to vindicate Warnstorf's species, especially when maintained by Johnson (1959). On examination, the latter gathering (in BO and L) clearly belongs to *S. perichaetiale*. It is most unlikely that *S. papillosum* should occur in the tropical zone, and deletion of *S. borneoense* from the tropical Asiatic flora is recommended.

ACKNOWLEDGMENTS

The author wishes to express his gratitude to : Mr R. Ross, Keeper of Botany (BM), for guidance in presentation and nomenclatural problems ; the Director and Dr A. Touw of the Rijksherbarium (L) for their hospitality and making available critical material ; Dr M. Rifai and Dr Chang Kiaw Lan for making available the early collections in the herbaria at Bogor (BO) and Singapore (SING) respectively.

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EXPLANATION OF PLATES

All plates, with the single exception of the light-micrograph, 40.B, are scanning electron-micrographs.

PLATE 37

A–E, *S. palustre* subsp. *pseudocymbifolium* :

A, dorsal leaf apex, × 200 ;

B, ventral leaf apex, × 200 ;

C, mid-ventral margin of branch leaf, × 200 ;

D, cortical leucocysts of branch (fragment of branch leaf base, above right) showing fibrils and pores, × 750 ;

E, dorsal surface of branch leaf, showing normal pores and pseudolacunae (arrowed), × 500.

F, *S. perichaetiale* : dorsal surface of branch leaf, showing occluded pseudolacunae (arrowed), × 750.

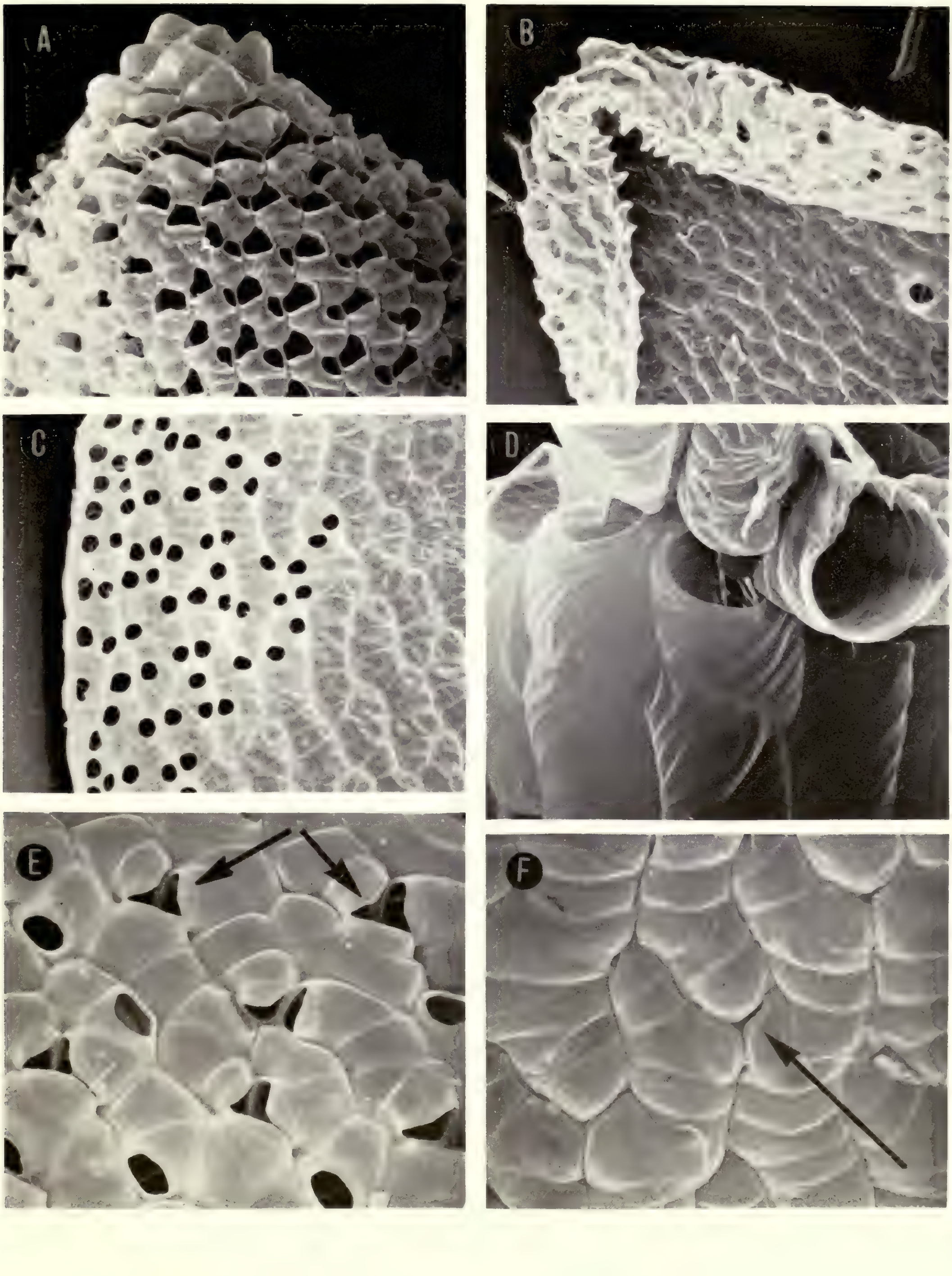

A
B
C
D
E
F

PLATE 38

A, *S. palustre* subsp. *pseudocymbifolium* : cortical leucocysts of stem, × 500.

B, *S. perichaetiale* : cortical leucocysts of stem, × 500.

C, *S. strictum* subsp. *pappeanum* ; ventral surface of branch leaf, showing apertures of pseudolacunae, × 750.

D, E, *S. luzonense* : ventral surface of branch leaf (note imperforate 'pseudopores'), D, × 500 ; E, × 1250.

F, *S. ceylonicum* : dorsal surface of branch leaf, showing free mid-line pores, × 500.

PLATE 38

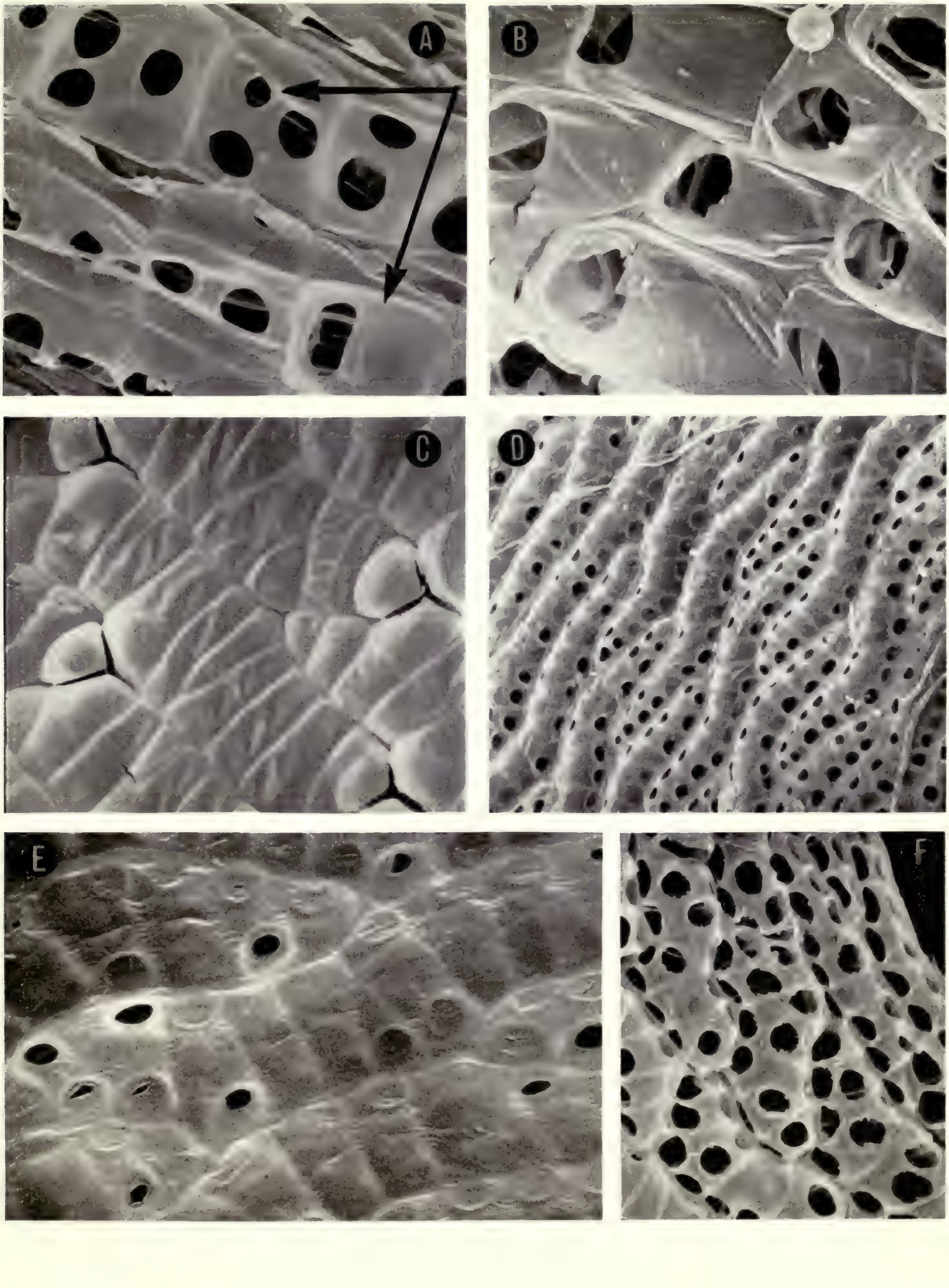


PLATE 39

A, B, *S. cuspidatulum* : A, dorsal surface of branch leaf, × 1000 ;
B, ventral surface of branch leaf, × 1000.
C, *S. cuspidatum* subsp. *subrecurvum* (form) : dorsal surface of branch leaf, × 500.
D, E, *S. junghuhnianum* : D, ventral margin of branch leaf, × 500 (compare Plate 37, C) ;
E, dorsal surface of branch leaf, × 500 (compare Plate 37, E).
F, *S sericeum* : dorsal surface of branch leaf, × 1000 (note collapse of efibrillose leucocysts).

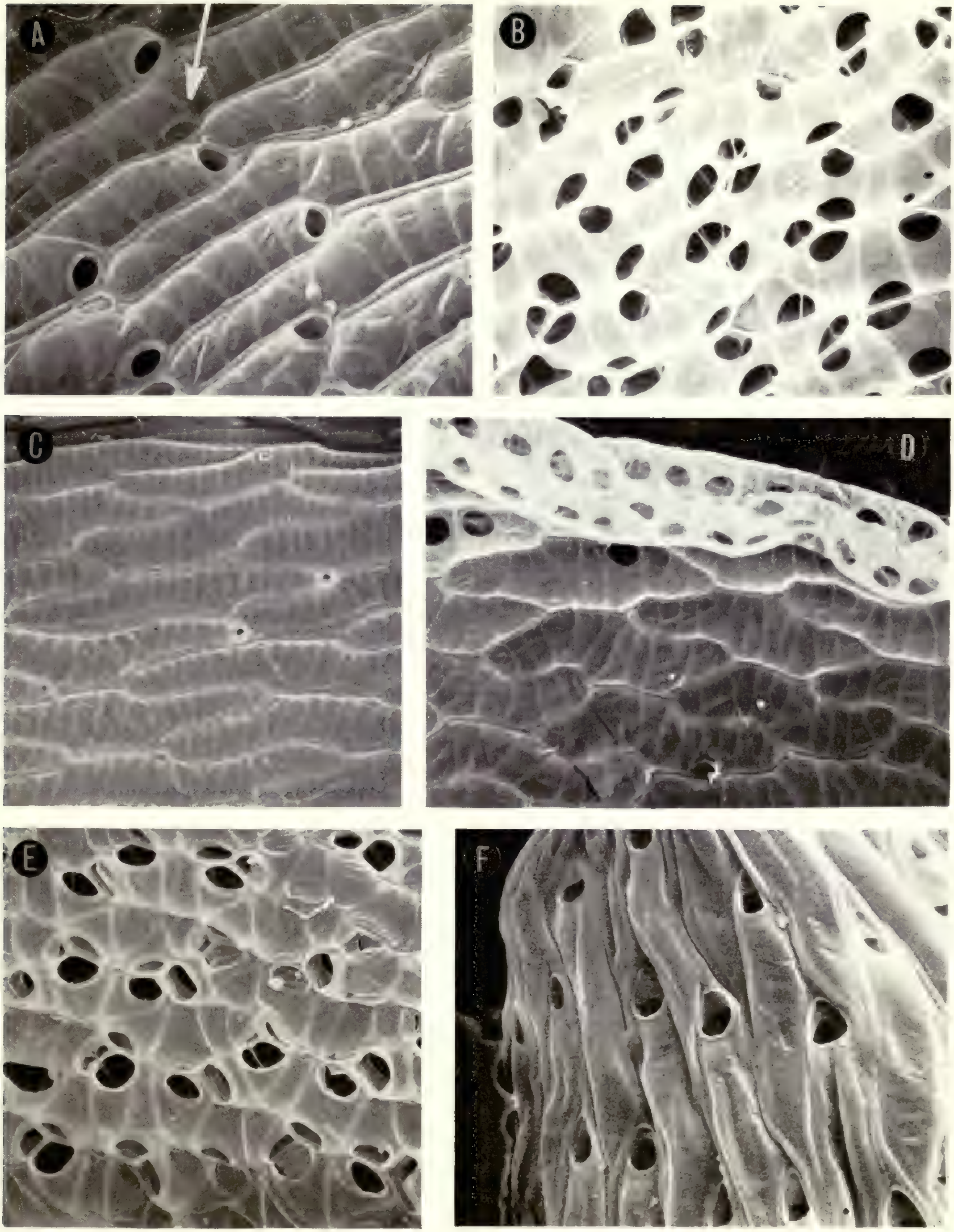
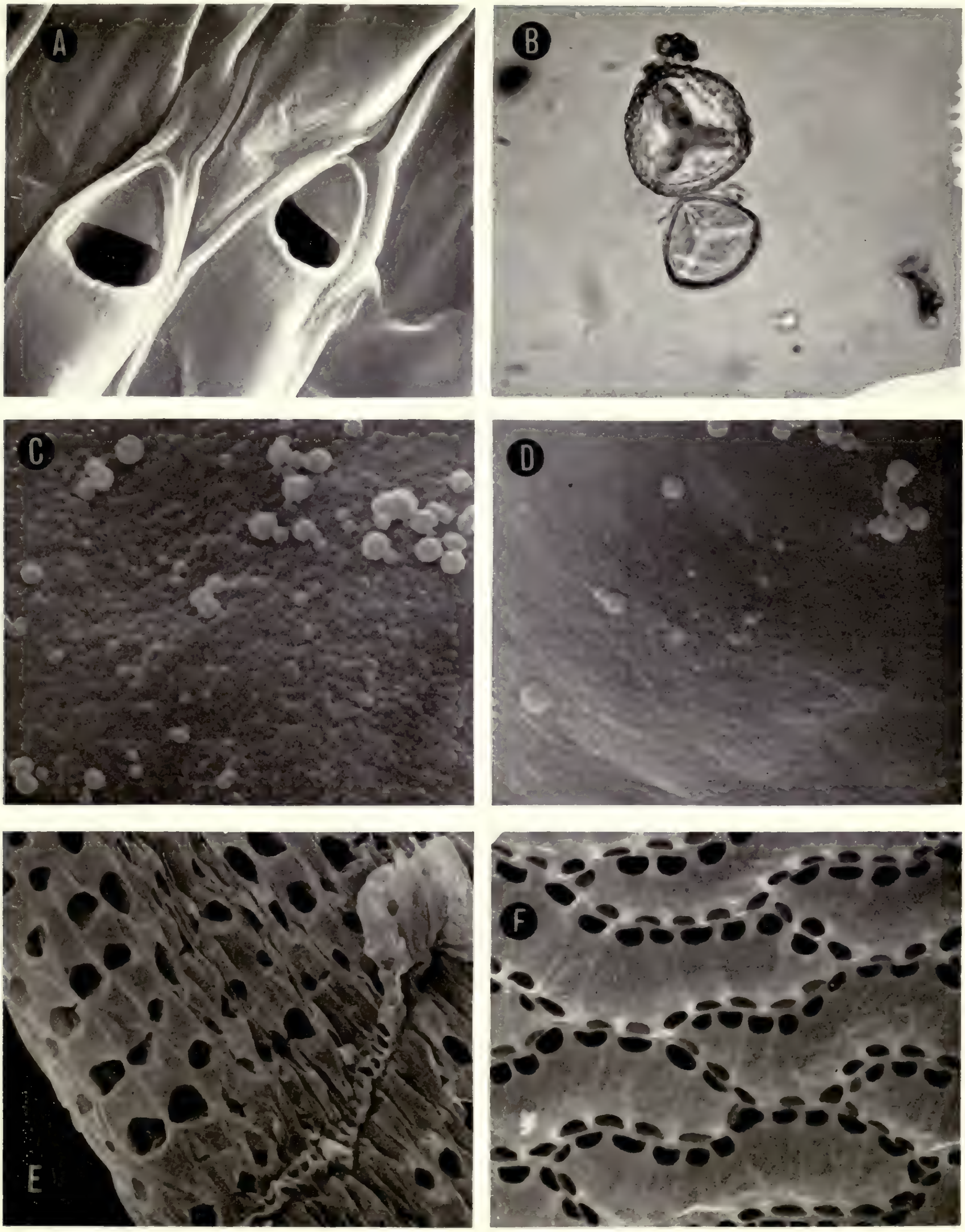

A
B
C
D
E
F

PLATE 40

A, *S. sericeum* : dorsal surface of branch leaf, × 2500.
B–D, *S. cuspidatum* subsp. *subrecurvum*.
B, spores, × 800 ;
C, 'macrospore' surface, × 10,000 ;
D, 'microspore' surface, × 10,000.
E, F, *S. ovatum* :
E, stem cortex, × 200 ;
F, dorsal surface of branch leaf, × 1000.


A
B
C
D
E
F

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